

***Yucca cernua* (Agavaceae) - New to the Louisiana Flora**

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ABSTRACT

The occurrence of the globally rare *Yucca cernua* (Agavaceae) is documented in Louisiana for the first time from an isolated region of Vernon Parish. *Published online www.phytologia.org Phytologia 104(1): 1-3 (March 22, 2022). ISSN 030319430.*

KEY WORDS: Agavaceae, endemic, isolated, Louisiana, rare plant, Vernon Parish, *Yucca*.

The genus *Yucca*, includes about 40-50 species of worldwide distribution and 28 in North America (Flora of North America (FNA) 2002). *Yucca* is notable for their rosettes of evergreen, tough, sword-shaped leaves and large terminal panicles of white or whitish flowers. They are native to the hot and dry (arid) parts of the Americas and the Caribbean. Recent field studies have resulted in the discovery of a specimen of *Yucca cernua* E.L. Keith from western Louisiana, which is herein reported as new to the state.

Yucca cernua E.L. Keith was described as an endemic restricted to a narrow band of acidic clay hills east of Jasper, Texas in Jasper and Newton Counties (Keith 2003; Poole et al. 2007). *Yucca cernua* in Texas is found in prairie and savanna openings in and along margins of pine-hardwood forests. *Yucca cernua* was not previously reported in Louisiana (Kartesz 2015; USDA 2021).

Yucca cernua was found in Louisiana on 27 February 2020 by Lee Wise with Hancock Forest Management (private timber management company) on a remote tract of land in western Vernon Parish (Figure 1-3). A few scattered vegetative individuals of *Yucca cernua* were documented in a small population. A single *Y. cernua* plant was observed flowering in early June of 2020. The *Y. cernua* site was documented along a utility line intersecting a loblolly pine (*Pinus taeda*) plantation. The soils that occur at the *Y. cernua* site are derived from the Bentley Geological Formation which overlies the Fleming Formation and are sandy clay loams developed along ridge lines. The site includes small natural openings. *Yucca cernua* was documented in association with primarily herbaceous flora, and the most abundant associated species was Missouri coneflower (*Rudbeckia missouriensis*). Missouri coneflower is often found in



Fleming Prairies which are highly restricted and globally rare prairies that follow the Fleming Formation paralleling Highway 63 between Jasper and Burkeville, Texas and eastward into Vernon Parish, Louisiana.

Missouri coneflower is a tallgrass prairie disjunct plant in Louisiana and has only been documented in Natchitoches and Vernon Parishes in Louisiana (Kartesz 2015, USDA 2021). The other commonly associated flora documented at the *Yucca cernua* site in Louisiana included *Ambrosia trifida*, *Ambrosia artemisifolia*, *Buchnera americana*, *Callirhoe involucrata*, *Coreopsis* sp., *Eriogonum* sp., *Linum* sp., *Monarda* sp., *Paspalum floridanum*, *P. plicatulum*, *Polytaenia nuttallii*, *Rubus* sp., and *Schizachyrium scoparium*. This assemblage of associated flora typically signifies that the former landscape that *Y. cernua* occurred in was an herbaceous prairie or pine savanna landscape.

Figure 1. *Yucca cernua* in flower and *Rudbeckia missouriensis* in background in Vernon Parish, Louisiana. Photo taken by Colton McKee.



Figure 2. *Yucca cernua* inflorescence in Vernon Parish, Louisiana. Photo taken by Colton McKee.



Figure 3. *Yucca cernua* basal leaves in Vernon Parish, Louisiana. Photo taken by Colton McKee.

Voucher specimen: **Louisiana**. Vernon Parish: From Evans High School off Hwy 111 in Evans, Louisiana, north on Hwy 111 for ca. 0.4 mi. to Burrell Harvey Rd. from jct of Burrell Harvey Rd. and Hwy 111 north on Burrell Harvey Rd. ca. 2.4 mi. to utility line crossing Burrell Harvey Rd. on east side of Burrell Harvey Rd., 8 July 2020, *Colton McKee* No. 1 (BAYLU).

Future investigation of this recently discovered *Yucca cernua* site is warranted. This would include documenting the extent of the population, information about reproduction, suggestions to future management, and locating additional potential sites in the adjacent region.

ACKNOWLEDGMENTS

We want to thank Hancock Forest Management for access to the site and documenting this plant species of greater conservation need.

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Descurainia kenheilii* (Brassicaceae): Revised description and new records from Colorado*Steve L. O'Kane, Jr.**Department of Biology, University of Northern Iowa
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steve.okane@uni.edu**Kenneth D. Heil**San Juan College, Farmington, New Mexico 87402
kendelheil@gmail.com**ABSTRACT**

Until recently, the only known collection of *Descurainia kenheilii* (Brassicaceae) was the holotype, a single, depauperate specimen from Stony Pass in San Juan County, Colorado. A revised description is provided based on recently examined specimens from the San Juan Mountains of Colorado. Herbarium specimens are cited to document the distribution of the species and a key is provided to separate it from *D. incana*. *Published online www.phytologia.org Phytologia 104(2): 4-7 (June 21, 2022). ISSN 030319430.*

KEY WORDS: *Descurainia kenheilii*, Brassicaceae, description, distribution.

In the summer of 1997 Ken Heil collected a diminutive member of the Brassicaceae in the tundra at the summit of Stony Pass, San Juan County, Colorado (Fig 1A). Unable to identify it, and thinking it was a species of *Draba*, he sent it to Ihsan Al-Shehbaz, an expert in the Brassicaceae, at the Missouri Botanical Garden. Al-Shehbaz determined that the miniature specimen, less than 1.5 cm tall, belonged to a new species of *Descurainia* and named it *D. kenheilii* in honor of its discoverer (Al-Shehbaz, 2007). In the years since, careful searches of the type locality, including by us, failed to find additional specimens of the species. Scott Smith, a talented amateur botanical sleuth from Colorado took on the challenge in 2021. He did not find any diminutive plants resembling *D. kenheilii* but did find much taller specimens of a species of *Descurainia* near the type locality that botanists have been calling *D. incana* (Fisch. & C. A. Mey.) Dorn (Fig. 1B, C). Thinking these specimens needed expert identification he sent them to Al-Shehbaz who recognized, based on characters of the fruits, ovules, pedicels, and duration, that they were taller, more robust, and as it turns out, typical members of *D. kenheilii*.

Using specimens housed primarily at San Juan College (SJNM) and supplemented by high resolution images of herbarium specimens available at SEINET (<https://swbiodiversity.org>), we have determined that *D. kenheilii* is limited to high elevations in the San Juan Mountains of southwestern Colorado. Below we provide an expanded description of the species, updated habitat information, a key to separate *D. kenheilii* from *D. incana*, representative specimens, and a distribution map of known specimens.

***Descurainia kenheilii* Al-Shehbaz, Harvard Pap. Bot. 12: 395, Fig. 1. 2007. TYPE: USA. Colorado. San Juan County:** San Juan Mountains, San Juan National Forest, top of Stony Pass, andesite porphyry and rhyolite tuff substrate, thin soil and talus slopes, alpine tundra, S20 Center & SW 1/4 T41N R6W, 12350 ft, 13 Sept 1997. *Heil 11505* (Holotype: SJNM; isotype: CS).

Revised description: **Short-lived perennials** (some biennial); eglandular; glabrescent to sparsely pubescent throughout with dendritic trichomes. **Stems** several, decumbent to suberect, branched basally mainly in the lower half with green leaves beyond the first year, mostly 1.4–11 dm, but when dwarfed, as in the holotype, unbranched and as little as 0.1 dm. **Basal leaves:** petiole (0.3–)3–40 mm; blade pinnate,

oblanceolate to obovate in outline, lateral leaflets 2–5 per side, (1–)1.2–6.5 × 0.5–1.5 cm, lateral leaflet lobes 2–4, pinnatifid, rounded. **Cauline leaves** subsessile, blade smaller distally, distal lobes narrower, surfaces sparsely pubescent to glabrescent. **Racemes** moderately to strongly elongated in fruit except not elongated in dwarfed plants as in the holotype. **Fruiting pedicels** ascending to erect, not appressed to the stem, straight, 1–7 mm. **Flowers:** sepals ascending, yellowish, ovate, 1–1.4 mm, pubescent; petals light yellow, narrowly oblanceolate, 1–1.5 × 0.3–0.4 mm; median filaments 0.6–1 mm; anthers broadly ovate, ca. 0.1 mm. **Fruits** siliques, ascending to erect, linear, sometimes a few curved, 5–12 × 1–1.3 mm, somewhat torulose, short-tapered at both ends, the ends rounded-acute to acute, valves each with a distinct midvein; septum with a distinct midvein (viewed at 10 \times magnification); ovules 4–8(–10) per ovary; style nearly obsolete, 0.1–0.3 mm, glabrous. **Seeds** uniseriate, reddish brown, oblong, 1–1.2 × 0.5–0.6 mm.

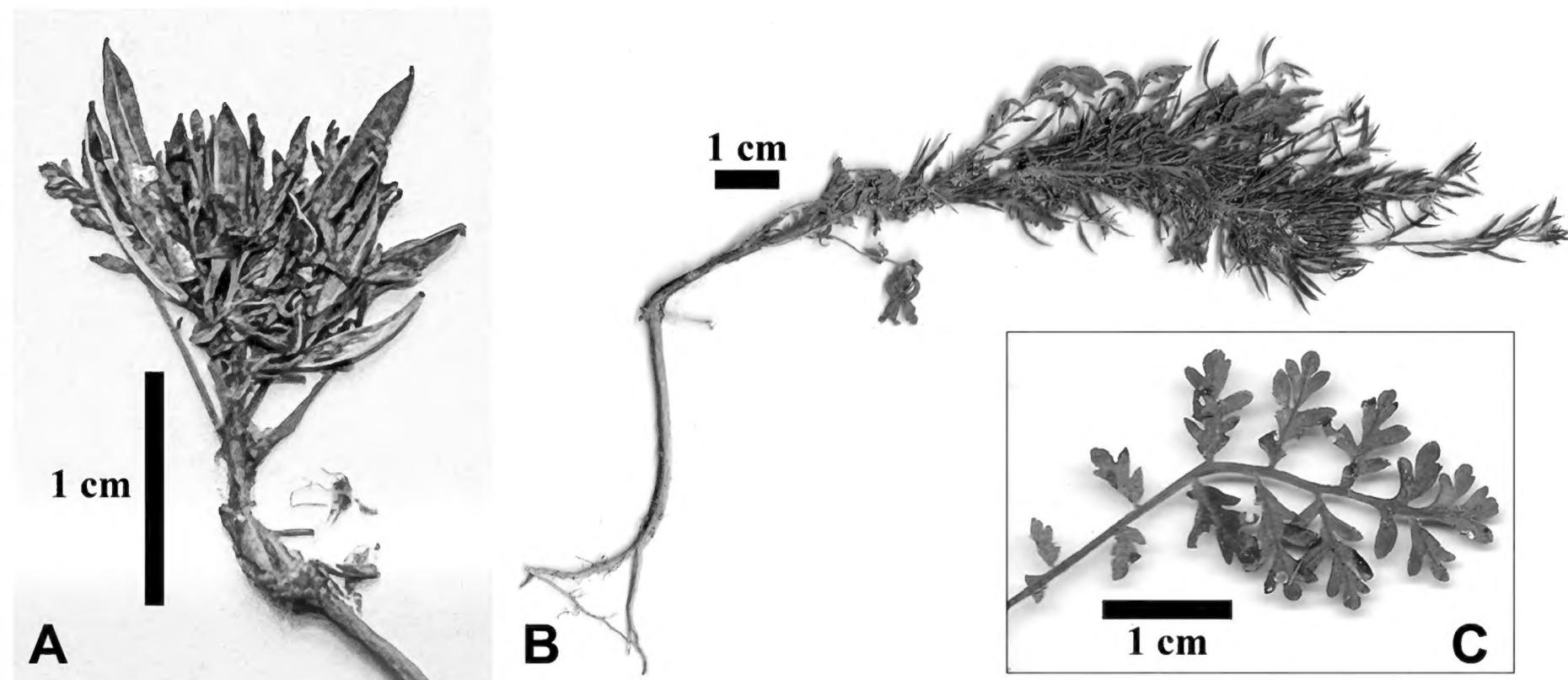


Figure 1. **A.** Diminutive specimen from the holotype. *Heil 11505* (SJNM). Photo Heil. **B.** One of two specimens collected from near the type locality. *Smith 0641* (MO). Photo Smith. **C.** Large basal leaf from second specimen. *Smith 0652* (MO). Photo Smith.

As noted by Al-Shehbaz (2007), interspecific hybridization and the ability to be weedy in disturbed situations makes the genus *Descurainia* taxonomically difficult. The specimens cited below appear to us to not involve hybridization. Several other specimens, however, seem to be intermediate between *D. kenheilii* and *D. incana*, in which case the two species may be difficult or impossible to distinguish.

Flowering Jul–Sep. Alpine tundra, talus slopes, and rock outcrops, in both undisturbed and disturbed areas; plants are taller and more robust where well-watered and with little competition; when found on species-rich, environmentally stressed tundra, plants may be dwarfed; 3150–3856 m (10330–12650 ft); San Juan Mountains of southwestern Colorado. *Descurainia kenheilii* is likely endemic to the San Juan Mountains of Colorado (Fig. 2), where it seems to replace *D. incana* at the highest elevations. The two species can be distinguished by the following key.

1. Plants short-lived perennials; branched from the base and nearly throughout; stems single or often several from the base, decumbent to erect; leaves green basally; elevations above 3150 m (10330 ft); ovules 4–8(–10) per ovary (examine several fruits and count funicles, not seeds); fruits somewhat torulose; fruiting pedicels divergent to ascending; fruits ascending to erect, not at all appressed to the stems.....***D. kenheilii***

1'. Plants biennial; mainly branched in the distal half of the stem; stems single, erect; leaves withered and deciduous basally; growing from low to high elevations; ovules (4–)6–22 per ovary; fruits nearly smooth

to torulose; fruiting pedicels ascending to erect; fruits erect, often nearly appressed to the stems, at least apically ***D. incana***

Representative specimens. **COLORADO.** **Conejos Co.:** End of Alamosa Can., below Treasure Falls, 37°22'N 106°40'W, 11200 ft. 28 June 1984. *Dixon* 3947 (ALAM). **Hinsdale Co.:** Weminuche Wilderness. Ca. 2 miles downstream of Weminuche Pass, along Los Pinos River, spruce-fir forest, growing in moss on north side of a large granite boulder, 37.6508333°N 107.3313889°W, 10450 ft., 3 Aug 2003. 3 Aug 2003. *O'Kane & Jamieson* 7473 (SJNM). **Mineral Co.:** San Juan National Forest, Pagosa Ranger District, Site 3, 37.43°N 107.08°W, 10350 ft. 24 Aug 1998. *Brinton* 36 (SJNM). **Rio Grande Co.:** Ca. 1 mile west of Summitville, 37°26'N 106°37'W, 11500 ft. *Dixon* 1916 (ALAM); ~7 miles NW of Platoro, vicinity of Elwood Pass & Cabin, 37.40414°N 106.63875°W, 11550 ft. 28 June 2013. *Sharples* 321 (COLO); Elwood Pass, 106°38'N 106°38'W, 11600 ft. 16 July 1981. *Dixon* 2943 (ALAM). **San Juan Co.:** BLM. West-facing slope of Sheep Mountain, ca 1.12 air miles south/southeast of Stony Pass and County Road 3, Alpine Tundra Community, 37.7843°N 107.5349°W, 12300 ft. 20 July 2021. *Heil* 37139 (FLD, SJNM); Plants on crushed volcanic rock-based soils, on road cuts east of Stony Pass, 37.789002°N 107.539076°W, 12300 ft. 23 July 2021. *Smith* 0641 and *Smith* 0642 (MO); San Juan National Forest/BLM ghost town, collections from around old homes, disturbed site with *Salix*, *Epilobium*, *Trisetum* and stinging nettles, 37.9311111°N 107.5708333°W, 22 Aug 2003. 22 Aug 2003. *Heil & Mietty* 22725 (SJNM); San Juan National Forest & BLM, ca. 3.5 air miles south/southeast of Howardville on County Road 3, near Stony Pass summit, base of Canby Mountain, alpine community, roadside along drainage, talus of igneous and metamorphic rocks, 37.79824°N 107.551149°W, 12500 ft. 15 July 2014. *Heil* 36413 (SJNM).



Figure 2. Distribution of *Descurainia kenheilii* in the San Juan Mountains of southwestern Colorado. Map generated using Google Maps.

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We thank Scott “Scotty” Smith for alerting us to his discovery and to Ihsan Al-Shehbaz for identifying Scotty’s discovery. We also thank Al-Shehbaz for fruitful discussions. Al-Shehbaz and Jennifer Ackerfield graciously reviewed the final manuscript.

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New to Oklahoma: *Decodon verticillatus* (Lythraceae)**Bruce Hoagland**

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ABSTRACT

Decodon verticillatus (L.) Elliott is a suffrutescent plant of wetland habitats that is common throughout much of the eastern United States. Although it is known from neighboring Arkansas and Texas, we report the first known population from Oklahoma. Approximately 15 plants were found on the Tiak District of the Ouachita National Forest west of Haworth, McCurtain County. *Published online* www.phytologia.org *Phytologia* 104(2): 8-9 (June 21, 2022). ISSN 030319430.

KEY WORDS: *Decodon verticillatus*, Lythraceae, Oklahoma

Decodon verticillatus (L.) Elliott is a suffrutescent plant common to wetland habitats in the eastern United States. The arching stems grow up to 2.5m and often root upon contact with the substrate (Vines 1960). The closest populations of *D. verticillatus* to Oklahoma occur in adjacent Little River and Sevier counties, Arkansas (Kartesz 2015). The population reported here was encountered on 7 October 2021 during a reconnaissance of wetland habitats in McCurtain County, Oklahoma. The accompanying photos illustrate the habitat (Fig. 1) and show emerging shoots of plants the following year (Fig. 2). Approximately 15 plants occurred in a partially shaded hillside seep located on an unnamed stream in the Tiak District of the Ouachita National Forest, approximately four miles west and three miles south of Haworth. Mature plants were in fruit. Associated species included *Acer rubrum*, *Alnus serrulata*, *Boehmeria cylindrica*, *Carex* sp., *Cephalanthus occidentalis*, *Hydrocotyle verticillata*, *Impatiens capensis*, *Juncus effusus*, *Osmundastrum cinnamomea*, *Saccharum giganteum*, *Saururus cernuus*, *Triadenum* sp., and *Woodwardia areolata*. Also present were 4-6 mature plants and several seedlings of *Triadica sebifera*. A voucher was collected and will be deposited in the Robert Bebb Herbarium (OKL) at the University of Oklahoma.

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Figure 1. Steep habitat containing *Decodon verticillatus*, McCurtain County, Oklahoma.



Figure 2. Emerging shoots of *Decodon verticillatus*, McCurtain County, Oklahoma. Photographed on 28 April 2022.

A new combination in *Heliotropium* (Boraginales: Heliotropiaceae)**Richard R. Halse and Christian Feuillet**

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ABSTRACT

The new combination *Heliotropium hartwegianum* (Steudel) Halse & Feuillet is made for a forthcoming volume of Flora North America North of Mexico. *Published online* www.phytologia.org *Phytologia* 104(2): 10 (June 21, 2022). ISSN 030319430.

KEY WORDS: *Heliotropium*, *Tournefortia*, Heliotropiaceae, new combination

Hilger & Diane (2003), in their molecular analysis of the Heliotropiaceae, showed that the large genus *Tournefortia* was polyphyletic. Species in *Tournefortia* sect. *Cyphocyema* are best treated as being in the genus *Myriopus* while species in *Tournefortia* sect. *Tournefortia* warrant inclusion within the genus *Heliotropium*. This position was followed by Craven (2005). One such species, *Tournefortia hartwegiana*, should be transferred to *Heliotropium* so that it may be included in the forthcoming treatment of the genus in Flora North America.

***Heliotropium hartwegianum* (Steudel) Halse & Feuillet, comb. nov.** Basionym: *Tournefortia hartwegiana* Steud. Nomencl. Bot. (ed. 2):693. 1841. = *Tournefortia undulata* Benth., Pl. Hartw. p. 20 & 346n. 1839. **LECTOTYPE** (here designated): Mexico. Jalisco. Bolaños, 1829. *Hartweg* 156, K [barcode K000478201]. Not *Tournefortia undulata* Ruiz & Pavon, Fl. Perur. 2:25. 1799. Not *Heliotropium undulatum* Vahl, Symb. Bot. 1:13. 1790. Synonym: *Tournefortia capitata* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11 (2): 332. **LECTOTYPE** (here designated): Mexico. Oaxaca, Sept. 1840, H.G. Galeotti 1260, BR [barcode BR 696805]; isolectotype G [barcode G00236227].

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Hilger, H. H. and N. Diane. 2003. A systematic analysis of Heliotropiaceae (Boraginales) based on *trnL* and *ITS1* sequence data. *Bot. Jahrb. Syst.* 125:19-51.

Phelipanche ramosa* (Orobanchaceae) in Louisiana*John Michael Kelley**Walter Jacobs Nature Park, Caddo Parks and Recreation
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ABSTRACT

Hemp broomrape is a noxious weed, native to Europe, which has invaded many areas around the globe. Here we provide the first report of this taxon in Louisiana where it inhabits roadsides in association with European weed species. *Published online www.phytologia.org Phytologia 104(2): 11-12 (June 21, 2022). ISSN 030319430.*

KEY WORDS: Noxious Weed, Louisiana, Caddo Parish, Invasive

Phelipanche ramosa (L.) Pomel, commonly called hemp broomrape (Fig. 1), is a holoparasitic herb in the Orobanchaceae which is becoming established in the southeastern United States (Weakley 2022). It has often been treated in the genus *Orobanche* (Weakley 2022). The species was probably introduced outside of Europe by cultivation of its host plants, such as *Cannabis*, *Medicago*, or *Trifolium* (PPQ 2019). It poses a minor threat to agriculture and spreads easily along mowed roadsides (PPQ 2019). It is a widespread pest in east Texas and is regularly observed on the citizen science application iNaturalist (Kartesz 2015). In early 2022, we found this species growing in Louisiana at broadly separated stations in Caddo, Jefferson Davis, and Lafayette parishes (not collected here). These apparently represent the first reports for the state (Kartesz 2015; MacRoberts 2006; Thomas and Allen 1996; USDA, NRCS 2021; Weakley 2022).

We found hemp broomrape growing along regularly mowed roadsides in association with ruderal, native herbs and European exotics. These included members of the genera *Trifolium*, *Medicago*, *Plantago*, *Lolium*, *Bromus*, *Solidago*, *Galium*, *Geranium*, *Sonchus*, *Veronica*, and *Lathyrus*. With abundant hosts and no intentional control efforts in Louisiana, this species will likely spread to other parishes. Hemp broomrape should be sought on weedy roadsides statewide, and in southern Arkansas.

Voucher specimens: **Louisiana. Caddo Parish:** Along Pine Hill road just west of Light Hill Baptist church, scattered plants with European weeds, 8 April 2022, John Michael Kelley s.n. (LSU), **Jefferson Davis Parish:** along highway 165 east of Iowa, clumps with clovers and sow thistle, 9 March 2022, Jacob Hamsher s.n. (LSU).

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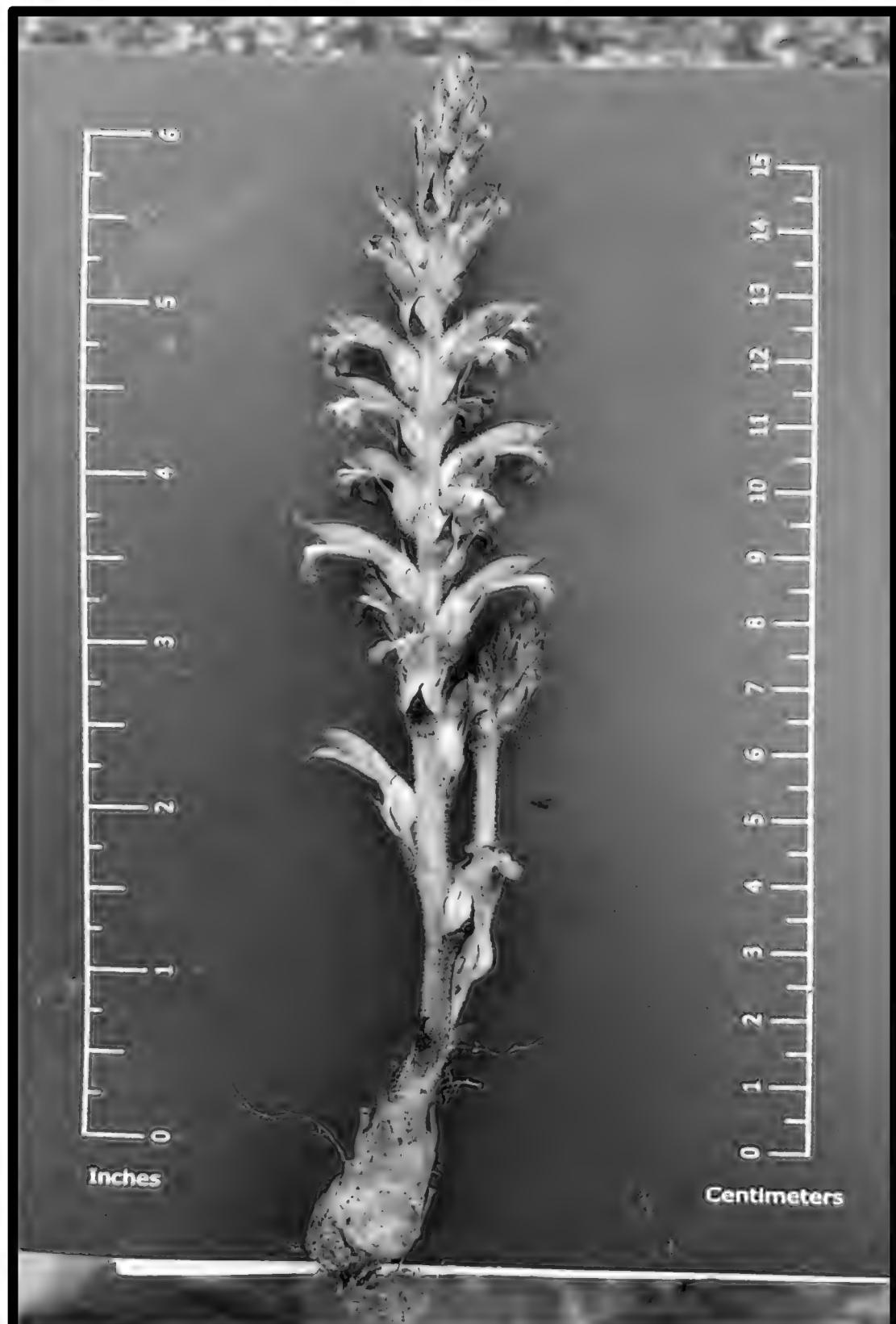


Figure 1. A typical plant of hemp broomrape.

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Isolated deciduous woodlands in central Texas

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ABSTRACT

The Edwards Plateau of central Texas is a physiographic region mostly in private ownership that includes grasslands, savannas, woodlands, and forests. Isolated deciduous woodlands on steep hillsides and deep limestone canyons contain populations of bigtooth maple (*Acer grandidentatum*, Aceraceae). We completed an aerial survey when leaves were changing colors in the fall to identify bigtooth maple populations. We used the quadrat procedure to estimate the density and basal area of trees and the density of juveniles. We found sixteen tree species in the overstory. Mean overstory density and basal area were 559 plants/ha and 33.4 m²/ha, respectively. In sequence Ashe juniper (*Juniperus ashei*) and bigtooth maple had the highest densities and were in the overstory of every community. Mean relative basal areas of these species were 5% and 43%, respectively, indicating the small size of Ashe juniper. We documented thirty understory woody species, and the mean density was 7,966 plants/ha. Sugar hackberry (*Celtis laevigata*) had the highest understory density, followed by Texas red oak (*Quercus buckleyi*), lacey oak (*Q. laceyi*), Ashe juniper, chinkapin oak (*Q. muehlenbergii*) and bigtooth maple. Juveniles of other species were scattered in various communities with high variation. Aerial photography and drone flights were very helpful finding these deciduous woodlands in part of this large physiographic region. *Published online www.phytologia.org Phytologia 104(3): 13-23 (September 20, 2022). ISSN 030319430.*

KEY WORDS: bigtooth maple, community composition, conservation, Edwards Plateau, herbivory, juniper, structure

Plants, plant community types, and animals were reported in logs kept by some travelers and Mexican soldiers during expeditions through south and central Texas from 1675–1691 (see Inglis 1964). They described some of the vegetation using common names and made comments about fires stretching across

the grasslands. While descriptions indicated tree-covered hills to the west and northwest, the edge of the central Texas Edwards Plateau region, the historical records of this time do not describe the diverse composition of species on the steep limestone hills or canyons of this area (Hill 1892). Early travelers did not traverse this central Texas region.

Much later, Palmer (1920) reported the diverse flora of these central Texas Canyon plant communities. Many publications incorrectly considered Texas a grassland (Sims 1988; Barbour and Billings 1988), which was true at times in the past but is not true today. Plant communities today include mixed juniper-oak (*Juniperus-Quercus*) woodlands, mesquite (*Prosopis*) woodlands, scrublands, savannas, grasslands, as well as riparian communities (Van Auken et al. 1979; Van Auken 1988, 2000; Elliott et al. 2014; Van Auken and Ford 2017; Van Auken 2018). Many studies more generally covered the plant species present in the broad area of central Texas but not the deciduous communities found in the steep-sided, narrow canyons (Tharp 1939; Gould 1969; Correll and Johnston 1979). Many of the central Texas plant communities have been studied more carefully recently (Van Auken et al. 1981; Amos and Gehlback 1988; Gehlback 1988; Van Auken and Ford, 2017; Van Auken 2018), but there are many unstudied species in these areas, and the extent of the communities are not well known, even today.

In addition to these plant communities changing with the retreat of glaciers and warming during the late Pleistocene or early Holocene, 12,000 to 15,000 years ago, community changes accelerated with the arrival of the European settlers and their animals starting about 400 years ago but increased dramatically in the past 100-200 years. Most grasslands changed dramatically but the woodlands did not change so much. The causes of the most recent grassland changes are debated. However, they include climate change, chronic high levels of herbivory, change in fire frequency and intensity, changes in species competitive ability, the spread of seed by livestock, small mammal populations, elevated levels of CO₂, or a combination of these factors (Van Auken 2000). The most accepted causes of the grassland changes seem to be the dramatic increase in domestic animals leading to heavy and continuous overgrazing, which influences wildfire frequency and intensity in central and western North American grasslands and prairies, including those in Texas (Collins and Wallace 1990). The product is the encroachment and spread of woody plants and the increase of woodland communities and their cover. There are still many grasslands in the Edwards Plateau region, especially in the western part, but there are many shrubs present in these communities. Changes in the central Texas woodlands is not as well studied.

Little ecological or population information is available concerning the species in these central Texas woodland communities (Van Auken 2018). Changes occurring in the last 100 years in these woodlands and savannas are not caused by lack of plant reproduction, seed maturation, or seedling emergence, which have not changed since the arrival of the European settlers (Collins and Wallace 1990). Recruitment failure seems to be caused by post-germination factors. Anecdotal reports suggest that the density of some woodland species is declining, possibly caused by browsing of white-tailed deer (*Odocoileus virginianus* Zimmerman) (McCorkle 2007). This will cause preferred plants to decrease in density and those resistant to herbivory will increase in density (Strole and Anderson 1992; Ruzicka et al. 2010).

Before recruitment success can be measured, the structure of the deciduous communities, both overstory and understory, must be known. We designed this study to answer the following research questions. Where do deciduous communities with high densities of bigtooth maple occur in central Texas? What is the overstory and understory composition and structure of these communities? Our study documents the species present, community composition, and maps the occurrence of some of these woodlands. We hypothesize that bigtooth maples occur in steep canyons which provide some reduction in temperatures. We hypothesize that bigtooth maple may be a preferred browse species for herbivores in this area, and therefore may be decreasing in density. We hypothesize that recruitment success of the other species present may be related to their palatability or nutritional value.

MATERIALS AND METHODS

Study Area

Viewing some deciduous communities with bigtooth maple (*Acer grandidentatum* Nutt.) in Texas is probably best in the Lost Maples State Natural Area, located in the southeastern part of the Edwards Plateau. However, similar canyons exist on private properties with deciduous woodlands and bigtooth maple that have not been documented (Carpenter and Brandimarte 2014). The current study was within the Edwards Plateau physiographic region of Central Texas on steep limestone hills and in deep canyons (Fig. 1).

The Edwards Plateau is a physiographic region described by geomorphology and is approximately 93,000 km². This diverse physiographic region includes woodlands, scrublands, savannas, grasslands and riparian communities and many rare and endemic species (Amos and Gehlbach 1988; Poole et al. 2007; Van Auken 2018). We studied eight deciduous woodlands, similar to those previously described (Van Auken et al. 1981), but having bigtooth maple. The herbaceous species in these communities were previously identified (Palmer 1920). The current study focuses on bigtooth maple populations within these unusual deciduous woodland communities. However, all trees and shrubs as well as juveniles of all woody species were identified and counted.

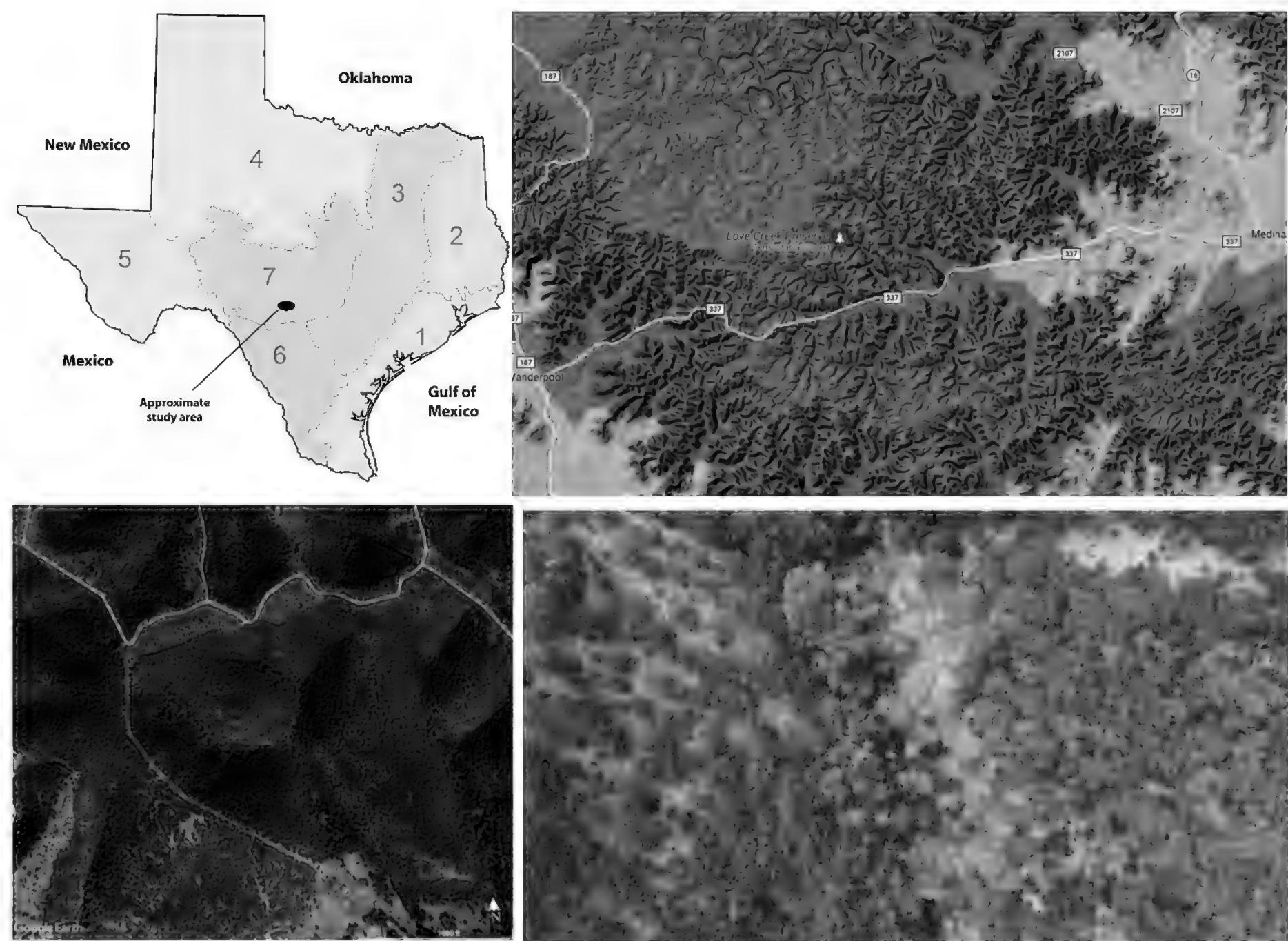


Figure 1. Top left, Texas in the southcentral United States, north of Mexico to the southeast. Black oval is the approximate location of the study area in the Edwards plateau region (area number 7). Top right is an expansion of the study area from the previous photo showing general topography. Bottom left, Google aerial imagery taken when bigtooth maple leaf color was most distinct and was used to first identify the deciduous communities. Bottom right, drone image of a deciduous woodland done while flying a DJI Inspire quadcopter.

The elevation of the study area is 484-614 m above mean sea level, and canyon bottom deciduous communities have deep calcareous silty clay soil (Mollisols over limestone bedrock, USDA NRCS 2017). The mean annual temperature is approximately 18.3°C, ranging from near 0.7°C in January to 34.1°C in August, and is highly variable. Mean annual precipitation is 72.4 cm/year with very little in July and August and highly variable, with May and September being wettest (NOAA 2018).

Imagery

At ground level, finding the deciduous communities in the juniper-live oak woodlands is difficult because of the small area covered by the deciduous communities and the rough terrain where they occur. However, the deciduous communities were easily identified from the air by the change of leaf color in the fall (Van Auken and Taylor 2017). We used google aerial imagery taken when bigtooth maple leaf color was greatest to identify and locate the deciduous communities (Fig. 1). We used drone flights and photography to identify the most accessible and largest deciduous communities. We conducted the drone survey when we could easily distinguish the deciduous species color from the juniper and oak. We completed the photography using a DJI Inspire quadcopter at an altitude of 100 m above ground level from the point of liftoff. This allowed orthoimagery coverage of each canyon where the deciduous communities occurred. Cloud cover was high, reducing shadow casts and image stitching errors. We set the camera ISO and shutter speed to auto to adjust based on conditions. We uploaded the captured imagery to Drone Deploy for stitching and then exported it as a georeferenced TIFF image. We then imported the TIFF to ArcGIS desktop software. Using the canopy color as a guide, we outlined the deciduous communities to create polygons, and we calculated the area using the ArcGIS measurement tools. We measured the ground sample areas, summed to get the actual total deciduous community area in hectares (ha), and we multiplied by the specific plant density in plants/ha to estimate the number of plants of each species in the canyon deciduous woodland communities studied (Van Auken and Taylor 2017).

Community Characteristics

We estimated the area of each deciduous community based on a drone survey. We used the mean density of the eight deciduous communities to calculate the density of each overstory and understory species in the canyon deciduous communities. Field conditions and site accessibility allowed ground surveying the deciduous woodlands containing the bigtooth maple woody plant population using the quadrat method (Van Auken et al. 2005). The number of 25 m² quadrats varied in each of the communities due to site size, variability, and topography. We determined adequate sampling using stabilization curves (not presented). We also determined relative occurrence (presence):

$$\% \text{ Occurrence} = \left(\frac{\text{species found} \times \text{number of communities}}{\text{total number of communities}} \right) \times 100$$

We sampled 356, 25 m² quadrats (0.885 ha) in the overstory deciduous communities and an area of 0.178 ha of the understory (5, 1 m² sub-quadrats in each of the 25 m² quadrats to count woody plants, one in each corner and one near the center). We used Correll and Johnston (1979) and USDA (2020) to identify the individuals. We counted and classified overstory as plants greater than 137 cm in height and 3 cm basal diameter. We classified woody plants less than 137 cm in height and/or 3 cm basal diameter as juveniles. We identified and calculated density, relative density, basal area, and relative basal area for each overstory species; we identified and calculated density for the understory species within each community (Van Auken et al. 2017).

RESULTS

Figure 2 shows some of the general community characteristics. We found sixteen woody species in the overstory of these communities with a mean of 7 species/community and a range of 5-12 species/community. Total density of overstory species in the communities examined ranged from 153

plants/ha to 1,024 plants/ha with a mean of 559 ± 599 plants/ha. Total understory density of juvenile woody plants ranged from 3,710 plants/ha to a high of 17,025 plants/ha with a mean of $7,963 \pm 9,125$ plants/ha. Total basal area of overstory species ranged from $27.1 \text{ m}^2/\text{ha}$ to $44.2 \text{ m}^2/\text{ha}$ with a mean of $33.8 \pm 4.8 \text{ m}^2/\text{ha}$. We found 30 woody species in the understories of the communities. The mean number of understory species was 15, with a range of 12 - 21 species (Fig. 2).

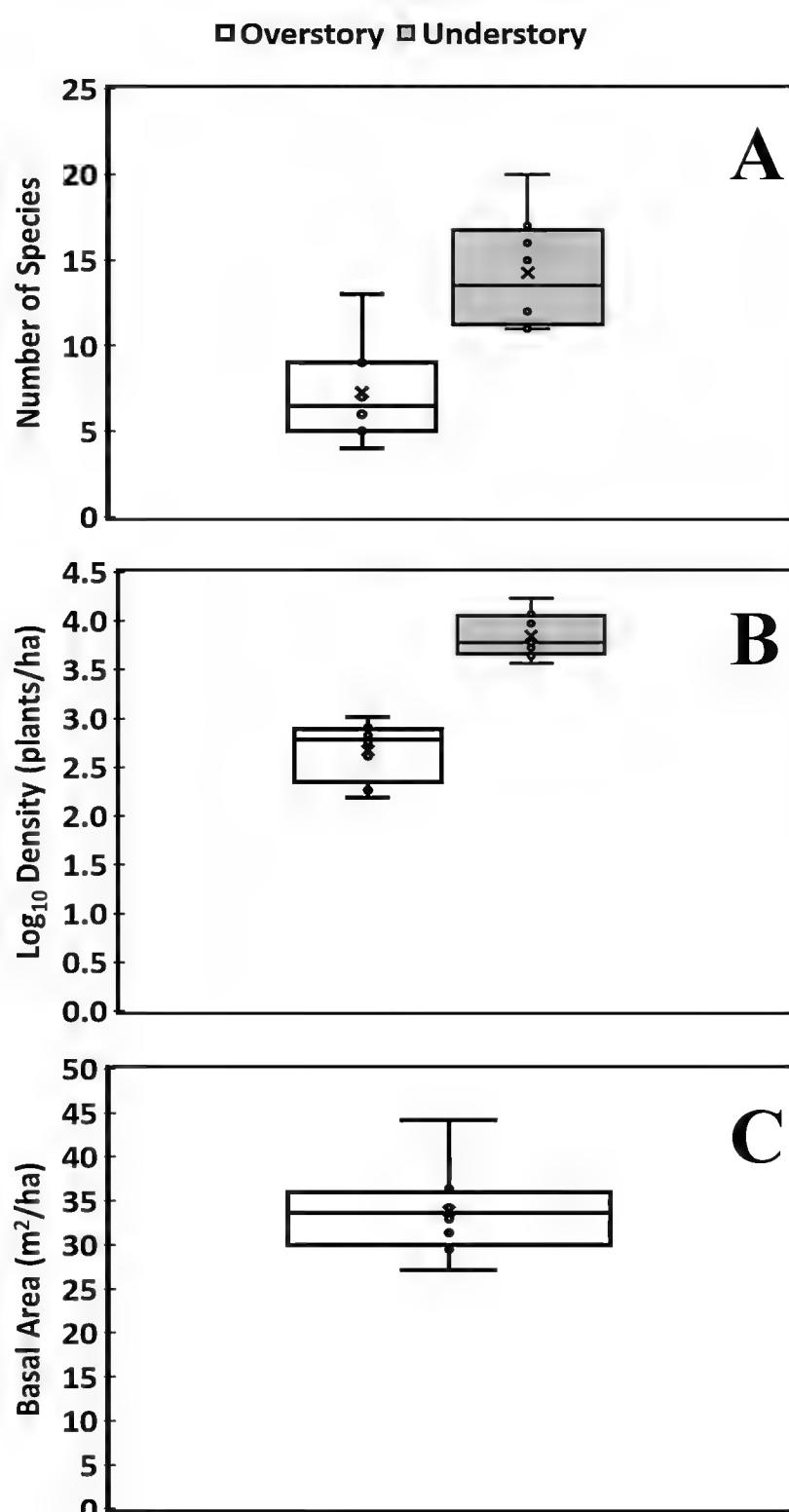


Figure 2. A comparison of the distributions of A) number of woody species and B) density (\log_{10}) for overstory (white) and understory (shaded) vegetation, and for C) the basal area of the overstory species. The x in the box represents the mean, the box extends from the 25th to the 75th quantile, the horizontal line within the box is the median, and the “whiskers” are 1.5 times the interquartile range. The mean number of overstory species is 7 ± 3 and 16 ± 3 are in the understory. The mean total density of the overstory is 559 ± 599 plants/ha and the understory is $7,963 \pm 4,563$ plants/ha. The mean overstory total basal area of all woody plants is $33.8 \pm 4.8 \text{ m}^2/\text{ha}$.

In the overstory, we found Ashe juniper (*J. ashei*) and bigtooth maple (*A. grandidentatum*) in every community sampled (100% occurrence, Table 1). Three species of oaks (*Quercus laceyi*, *muhlenbergii*, and *buckleyi*) were the next most common species (50-63% occurrence). Texas black walnut (*Juglans major*) also had an occurrence of 63%, but other species were at 50% or less (Table 1). Ashe juniper and bigtooth maple had the highest mean density at 221 ± 179 and 169 ± 73 plants/ha, respectively, out of a total mean density of 559 plants/ha (Table 1). Their mean relative density was 40 and 30%, respectively. Bigtooth maple had the highest basal diameter ($9.6 \pm 4.7 \text{ m}^2/\text{ha}$) and accounted for the largest relative basal area of 43%. Chinkapin oak and Lacey oak also had high basal areas of 6.1 ± 6.1 and $4.4 \pm 7.4 \text{ m}^2/\text{ha}$ (25 and 18% relative basal area), respectively. Ashe junipers were smaller individuals with a mean basal area of $1.3 \pm 1.8 \text{ m}^2/\text{ha}$ (relative basal area of 5%; Table 1).

We found four understory species in all of the communities examined (occurrence = 100%) including sugar hackberry (*C. laevigata*), Texas red oak (*Q. buckleyi*), Ashe juniper (*J. ashei*), and Texas persimmon (*Diospyros texana*) (Table 2). Eight species had 75-88% occurrence including bigtooth maple (Table 2).

The mean density of the species with 100% occurrence ranged from 602 to 1201 plants/ha (Table 2). The species with 75-88% occurrence had mean density values from 138 to 926 plants/ha (Table 2). We found other species in at least one community with a density as low as four plants/ha.

Table 1. Woodland overstory species (scientific and common names) as well as percent occurrence, mean density (plants/ha; $1 \pm$ standard deviation), relative density, mean basal area (m^2/ha ; $1 \pm$ standard deviation), and relative basal area. Species are ranked from high to low (top to bottom) based on mean density.

OVERSTORY						
Scientific name	Common Name	% Occur.	Density (plants/ha)	Relative Density (%)	Basal Area (m^2/ha)	Relative Basal Area (%)
<i>Juniperus ashei</i>	Ashe juniper	100	221 \pm 179	40	1.3 \pm 1.8	5
<i>Acer grandidentatum</i>	Bigtooth maple	100	169 \pm 73	30	9.6 \pm 4.7	43
<i>Quercus laceyi</i>	Lacey oak	63	41 \pm 60	7	4.4 \pm 7.4	18
<i>Quercus muehlenbergii</i>	Chinkapin oak	50	26 \pm 28	5	6.1 \pm 6.1	25
<i>Sophora secundiflora</i>	Mt. laurel	38	23 \pm 44	4	< 0.1	< 1
<i>Diospyros texana</i>	Texas persimmon	50	20 \pm 29	4	< 0.1	< 1
<i>Vitis arizonica</i>	Arizona grape	38	14 \pm 25	3	< 0.1	< 1
<i>Juglans major</i>	Tx. black walnut	63	10 \pm 10	2	0.4 \pm 0.6	2
<i>Fraxinus albicans</i>	Texas ash	50	9 \pm 10	2	0.9 \pm 0.9	4
<i>Prunus serotina</i>	Black cherry	25	6 \pm 12	1	0.7 \pm 1.2	3
<i>Ungnadia speciosa</i>	Mex. Buckeye	25	5 \pm 9	1	0.1 \pm 0.3	< 1
<i>Quercus buckleyi</i>	Texas red oak	50	5 \pm 6	1	0.3 \pm 0.5	1
<i>Sideroxylon lanuginosum</i>	Gum bumelia	25	5 \pm 11	1	< 0.1	< 1
<i>Aesculus pavia</i>	Red buckeye	13	2 \pm 6	< 1	< 0.1	< 1
<i>Celtis laevigata</i>	Sugar hackberry	13	1 \pm 2	< 1	< 0.1	< 1
<i>Tilia caroliniana</i>	Carolina basswood	13	1 \pm 3	< 1	0.2 \pm 0.6	1
Total			559	99	24.5	98

DISCUSSION

This descriptive study of deciduous woodlands in the Edwards Plateau in central Texas indicates a relatively diverse community for this area. These eight deciduous woodlands are ecologically similar to deciduous woodlands described in other areas of the Edwards Plateau (Van Auken et al. 1981; Gehlbach 1988), and similar to the communities reported in the upper canyons of this area (Palmer 1920). Differences between communities included 16 woody species (trees or shrubs) found in the current study while 19 were reported in the previous study (Van Auken et al. 1981). Chinkapin oak (*Q. muehlenbergii*), bigtooth maple (*A. grandidentatum*), gum bumelia (*Sideroxylon lanuginosum*), and Carolina basswood (*Tilia caroliniana*) were not found in the previous study. Blue sage (*Salvia ballotiflora*, shrub) was not found in the current study. Other notable differences in plant species between the two studies included lower density of Texas persimmon (*Diospyros texana*) in the current study when compared to the previous study; and a lower density of Lacey oak (*Q. laceyi*) and Texas red oak (*Q. buckleyi*, formerly *Q. texana*) in the present study.

Over all woody plant density was lower in the current study when compared to the earlier study (Van Auken et al. 1981). There may be several reasons which would explain these differences. The current study focused on communities in canyons which are at a lower elevation and more shaded than the north

facing slopes of the previous study, which may be as much as 150 meters higher. Further, the communities in the first study were 40-50 km further southeast (closer to the southern edge of the physiographic Edwards Plateau region), were brushy, and probably drier. All studies were on private property and as ownership changed land management changed (Carpenter and Brandimarte 2014). Methodology was slightly different between the two studies, with multi-stem species (red buckeye; *Aesculus pavia*) counted per stem (first study) rather than per clump. The deciduous woodland communities in the current study were very open, with few large understory shrubs. Understory density was high in most of the current communities studied, but the woody plants were mostly less than 10 cm tall. In the understory of the current study there were 30 woody species including 16 juvenile tree species, 10 shrubs, and 4 woody vines (Table 2). The previous study did not measure the understory plants.

Table 2. Understory woody species (scientific and common names) as well as percent occurrence, mean density (plants/ha; 1 \pm standard deviation), and relative density. Species are ranked from high to low (top to bottom) based on mean density.

UNDERSTORY					
Scientific name	Common name	% Occurrence	Mean density	SD	% Density
<i>Celtis laevigata</i>	Sugar hackberry	100	1201 \pm	2450	15
<i>Quercus buckleyi</i>	Texas red oak	100	1059 \pm	430	13
<i>Quercus laceyi</i>	Lacey oak	88	926 \pm	941	12
<i>Juniperus ashei</i>	Ashe juniper	100	667 \pm	753	8
<i>Quercus muehlenbergii</i>	Chinkapin oak	75	658 \pm	704	8
<i>Acer grandidentatum</i>	Bigtooth maple	88	642 \pm	700	8
<i>Diospyros texana</i>	Texas Persimmon	100	602 \pm	445	8
<i>Parthenocissus quinquefolia</i>	Virginia creeper	88	386 \pm	545	5
<i>Sideroxylon lanuginosum</i>	Gum bumelia	63	273 \pm	519	3
<i>Vitis arizonica</i>	Arizona grape	75	257 \pm	307	3
<i>Smilax bona-nox</i>	Saw greenbriar	88	249 \pm	234	3
<i>Sophora secundiflora</i>	Mountain laurel	50	241 \pm	370	3
<i>Ungnadia speciosa</i>	Mexican buckeye	50	204 \pm	412	3
<i>Fraxinus albicans</i>	Texas ash	88	158 \pm	188	2
<i>Prunus serotina</i>	Black cherry	88	138 \pm	106	2
<i>Ilex decidua</i>	Possumhaw holly	13	99 \pm	279	1
<i>Juglans microcarpa</i>	Arizona walnut	63	46 \pm	70	1
<i>Ulmus crassifolia</i>	Cedar Elm	13	37 \pm	104	1
<i>Mahonia trifoliolata</i>	Agarita	25	26 \pm	57	<1
<i>Rhamnus caroliniana</i>	Carolina basswood	25	24 \pm	50	<1
<i>Toxicodendron radicans</i>	Poison Ivy	25	12 \pm	30	<1
<i>Ptelea trifoliata</i>	Hop tree	13	11 \pm	31	<1
<i>Tilia caroliniana</i>	Carolina buckthorn	13	10 \pm	28	<1
<i>Styphnolobium affine</i>	Eve's necklace	13	7 \pm	19	<1
<i>Ageratina havanensis</i>	Shrubby boneset	13	7 \pm	19	<1
<i>Cercis canadensis</i>	Redbud	25	6 \pm	11	<1
<i>Yucca rupicola</i>	Twisted-leaf yucca	13	6 \pm	16	<1
<i>Baccharis neglecta</i>	Roosevelt weed	13	6 \pm	16	<1
<i>Rhus virens</i>	Evergreen sumac	13	4 \pm	10	<1
<i>Styrax platanifolius</i>	Sycamore leaf snowbells	13	4 \pm	10	<1
Total			7963		99

We were interested in describing the composition and structure of these communities, which is a gap in knowledge. There are reports suggesting population declines of many deciduous species in the Edwards Plateau possibly caused by browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) (McCorkle 2007; Boerne Chapter of the Native Plant Society of Texas 2015; Nelson-Dickerson and Van Auken 2016; Van Auken and Taylor 2021).

The loss of most large vertebrate predators in the Edwards Plateau region of Texas caused populations of white-tailed deer to become the major large herbivores in the area. Estimates suggest white-tailed deer are at or above carrying capacity causing negative impacts on vulnerable plant populations (Fulbright and Ortega-S. 2008; Wolverton et al. 2007). Browsing by white-tailed deer has been suggested as a major factor in recruitment failure in populations of Texas red oak, eastern black cherry and Texas ash (*Q. buckleyi*, *P. serotina* and *F. albicans*) favoring increased density and biomass of ash juniper (Russell and Fowler 2004; Van Auken 1988). The same seems to be true for bigtooth maple (Nelson Dickinson and Van Auken 2016; Van Auken and Taylor 2021).

Density values presented in the current document represent the mean number of woody plants found in the quadrates measured as plants per hectare. We estimated the total area of the deciduous communities surveyed to be 9.56 ha. Mean density values presented are per hectare and if the plants are equally found through the deciduous communities examined, the actual number of plants of a given species would be expected to be 9.56 times higher because of the total area of the deciduous woodlands. Some comparisons are indicated below but all are in the table (Table 3).

Table 3. Woodland community overstory species (scientific and common names) as well as calculated density (actual density in plants/hectare X measured community area in hectares) and community understory density. Species are ranked from high to low (top to bottom) based on mean overstory density.

Scientific name	Common Name	Estimated whole community overstory density	Estimated whole community understory density
<i>Juniperus ashei</i>	Ashe juniper	2,113	6,176
<i>Acer grandidentatum</i>	Bigtooth maple	1,616	5,945
<i>Quercus laceyi</i>	Lacey oak	392	8,575
<i>Quercus muehlenbergii</i>	Chinkapin oak	249	6,693
<i>Sophora secundiflora</i>	Mt. laurel	220	2,232
<i>Diospyros texana</i>	Texas persimmon	191	5,575
<i>Vitis arizonica</i>	Arizona grape	134	2,380
<i>Juglans major</i>	Texas black walnut	96	426
<i>Fraxinus albicans</i>	Texas ash	86	1,463
<i>Prunus serotina</i>	Black cherry	57	1,278
<i>Ungnadia speciosa</i>	Mex. buckeye	48	1,889
<i>Quercus buckleyi</i>	Texas red oak	48	9,806
<i>Sideroxylon lanuginosum</i>	Gum bumelia	48	2,528
<i>Aesculus pavia</i>	Red buckeye	20	0
<i>Celtis laevigata</i>	Sugar hackberry.	10	11,121
<i>Tilia caroliniana</i>	Carolina basswood	10	93

These whole community density values suggest that there are 11,121 sugar hackberry juveniles in the understory of these deciduous communities and we only found one mature tree/ha in the overstory and estimated 10 in the whole community (Table 3). There were 25,074 oak juveniles found in the understory (three species) with 72 overstory plants/ha or 689 trees in the whole community. For Ashe juniper, there

were 221 plants/ha (highest mean tree density) and 2,113 expected for the entire deciduous community. In the understory the mean for juniper juveniles was 667 plants/ha, while the estimated number for the deciduous woodland community was 6,176, which was the fourth highest juvenile woody plant.

Bigtooth maple, our main species of interest in these deciduous woodlands, had an overstory mean density of 169 plants/ha. Expanding this density to the area of the entire deciduous woodland indicated 1,616 bigtooth maple trees. Understory bigtooth maple juvenile density was 642 plants/ha or expanded to the deciduous woodland, the density of juveniles would be 5,945 plants. At this density, it would seem that there would be sufficient numbers for adequate recruitment to maintain the adult population. However, there were no saplings reported in a previous study and none in this study (Nelson-Dickerson and Van Auken 2016).

Although many more potential deciduous woodland communities were observed in the satellite imagery, the ability to fly the UA in these areas was limited because of FAA rules. Without accessible roads close enough to the deciduous woodland community, these areas were not flown because the drone could not be seen constantly. Consequently, 26 flights were done over deciduous woodlands detected in the satellite imagery. Of those, 23 produced imagery worthy of further evaluation. Out of the 23 sites, 10 were selected for ground surveys. Based on walking through all ten, two of the ten sites selected did not have bigtooth maple trees and were not quantitatively surveyed. The remaining eight were surveyed, all contained adult bigtooth maples and all but one had juveniles.

The deciduous woodland communities identified and examined in the current study were similar to deciduous woodland communities identified in the past (Van Auken et al. 1981) but had bigtooth maple trees. We found and report a few species that were not previously described from these communities. In spite of examining a large area, the number of individual woody species was relatively small compared to wetter or more tropical areas (Mutke and Barthlott 2005; or see Keddy 2017). We could tell if a specimen was juvenile (non-reproductive) or mature, but not the specific age. In addition, time of loss or age when adults were lost was not obvious. Consequently, additional study will be necessary to understand the stability or lack of stability of these unusual communities.

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Symphyotrichum ericoides* (Asteraceae) in Louisiana*John Michael Kelley**

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ABSTRACT

Symphyotrichum ericoides is reported for Louisiana, where it is known from a single calcareous prairie in the Morse Clay system. *Published online* www.phytologia.org *Phytologia* 104(3): 24-26. (September 20, 2022). ISSN 030319430.

KEY WORDS: *Symphyotrichum*, Asteraceae

In the course of ongoing research on Louisiana's grasslands, I located a small Morse Clay calcareous prairie, apparently not surveyed by previous explorers (MacRoberts et al. 2009). After consulting the landowners, I began my floristic survey of a 4 ha exposure of alkaline soils with a particular focus on one less-disturbed 0.5 ha opening. Within this smaller area I discovered *Symphyotrichum ericoides* (L.) G.L.Nesom in September 2021 (Figs. 1 and 2). Hundreds to a few thousand plants were growing in the opening and a few individuals were found in a field on the adjacent property.

S. ericoides is native to prairies, glades, and disturbed openings in the northern and central United States and occurs sporadically in the Southeast (Brouillet et al. 2006, Weakley 2020). It has been deleted and excluded from the Louisiana flora by major sources (Gandhi and Thomas 1989, Kartesz 2014; SERNEC 2020; USDA 2014; Weakley 2020). I identified it by its small, bluish, falcate leaves which wither on the lower stem before flowering, strigose pubescence on leaves and stem, and phyllaries tipped with whitish spines.

The flora of this site will be discussed in a future publication, but particular associates might prove useful to surveyors. This prairie opening represents a drier than average phase of the Morse clay system which I have studied in Louisiana and Arkansas. It is marked by the presence of *Callirhoe papaver*, *Pyrrhopappus pauciflorus*, *Onosmodium bejariense*, *Asclepias viridiflora*, *Salvia azurea* and *Symphyotrichum oolentangiense* (pers. obs.). I have searched nearby sites with these species without locating additional *S. ericoides*. The species deserves tracking, with a suggested state rank of "S1 (critically imperiled)", but deeper review of herbarium specimens should be undertaken. The landowner is cooperative and will work to preserve the population.



Figure 1. *S. ericoides* habitat in December 2021. Tall grasses include *Sorghastrum*, *Schizachyrium* and *Andropogon*. Dark area at lower right is dominated by *Iva* and *S. ericoides*.



Figure 2. *S. ericoides* plant from the Louisiana population with withered caudine leaves and close-ups illustrating pubescence on the leaves and spine-tipped phyllaries.

Voucher. **Louisiana. Bossier Parish:** Marbleseed Meadow, ~300 plants, colonial, East side of opening, with *Sorghastrum*, *Dichanthelium*, *Ruellia*, *Salvia*, *Iva*, etc., 32.40, -93.40, 7 Oct 2021, Kelley s.n. (LSU).

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***Sertulum Ternstroemiacearum*, V. Taxonomy of the *Ternstroemia dentata* complex,
including one new species**

Sertulum Ternstroemiacearum, V. Taxonomía del complejo *Ternstroemia dentata*,
incluyendo una nueva especie

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ABSTRACT

Ternstroemia Mutis ex L.f. (Ternstroemiaceae) presents its greatest center of diversity in northern South America, where *T. dentata* (Aubl.) Sw., one of the most common species, occurs. As a result of a critical review of herbarium specimens of this and most related taxa, a new taxonomic concept (*T. ostracophylla* J.R. Grande, *sp. nov.*) is proposed. A complete description of the new entity and a table where it is compared with *T. dentata*, *T. laevigata* and *T. urophora* are provided. Illustrations, distribution maps, conservation status, and a discussion of the affinities and ecology of these four species are provided along with a key and a complete list of specimens. *Published online www.phytologia.org Phytologia 104(3): 27-39 (September 20, 2022). ISSN 030319430.*

KEY WORDS: Brazil, Colombia, Guayana Shield, South America, Taxonomic novelty, Ternstroemiaceae, Venezuela.

RESUMEN

Ternstroemia Mutis ex L.f. (Ternstroemiaceae) presenta su mayor centro de diversidad en el norte de Sudamérica, donde una de sus especies más comunes es *T. dentata* (Aubl.) Sw. Como resultado de la revisión crítica de muestras de herbario de este y los taxones más relacionados, se propone un nuevo concepto taxonómico (*T. ostracophylla* J.R. Grande, *sp. nov.*). Se proporciona una descripción completa de la nueva entidad y una tabla donde se compara con *T. dentata*, *T. laevigata* y *T. urophora*. Se proporcionan ilustraciones, mapas de distribución, estado de conservación y una discusión sobre las afinidades y la ecología de estas cuatro especies junto con una clave y una lista completa de especímenes.

PALABRAS CLAVE: Brasil, Colombia, Escudo Guayanés, Sudamérica, Novedad taxonómica, Ternstroemiaceae, Venezuela.

Ternstroemia Mutis ex L.f. (Ternstroemiaceae or Pentaphylacaceae s.l.) includes *ca.* 100-150 species from tropical America, continental tropical Africa, India, Sri Lanka, China, Southeast Asia, Australia, the Korean peninsula, and Japan (Kobuski 1942a, b, 1943; Barker 1980; Stevens 2001–onwards; Luna and Ochoterena 2004; Weitzman et al. 2004; Min and Bartholomew 2007; Cheek et al. 2017; Grande 2019; POWO 2022). One of them, *Ternstroemia gymnanthera* (Wight & Arn.) Bedd., is cultivated and has become naturalized in the U.S.A. (Christman 2008 [2015]; Serviss and Peck 2008). The genus is characterized by having a bushy or arboreal habit, glabrous (except in *Ternstroemia pubescens* Kobuski), alternate, and coriaceous or chartaceous leaves, with serrate, toothed or sub-entire margins, showing corky warts on the abaxial surface. Its flowers are axillary and solitary, with a quincuncial perianth, fleshy petals with membranous margins, more or less fused towards the base, and numerous stamens, subequal to dimorphic, arranged in one to several series. The anthers are bilocular and apiculate, with basal insertion, and the pistil differentiates into a superior ovary, 1–3 (–4–8) locular, with 1–numerous ovules per locule, a

styloid (consisting of a short style, entire or 2–3-divided, plus the prolonged apex of the ovary) and one to several stigmata, which may be punctiform, capitate (referred as “subpunctiform” in Rodríguez-Duque et al. 2021) or peltate. The fruits are cartilaginous, with circumcise or subvalvular dehiscence, and seeds are relatively large (usually greater than 4 mm long), covered by a fleshy testa that turns red or fuchsia when ripe (Metcalfe and Chalk 1957; Weitzman et al. 2004; Grande 2018, 2019, 2020 [2021]).

Taxonomy of *Ternstroemia* has received increasing attention in recent years, with new species descriptions and regional revisions mainly from the Neotropics (e.g., Santamaría et al. 2014; Grande 2019; Vieira 2020) and Africa (Cheek et al. 2017, 2019). After a recent Ph.D. dissertation on Guayana Shield species (Grande 2019), probably the region with the highest diversity in the genus, several species complexes were proposed. One of them, widespread through northern South America, is formed by *Ternstroemia dentata*, *T. laevigata*, *T. urophora* and an additional undescribed species. In advance to the revision of the tribe *Ternstroemieae*, in progress since 2009 (<https://www.researchgate.net/project/Systematics-of-tribe-Ternstroemieae-worldwide>), the taxonomy and distribution of the *Ternstroemia dentata* complex is updated.

MATERIALS AND METHODS

Approximately 1000 collections (for a total of *ca.* 1500 dried specimens) from northern South America, including loans from herbaria B, F, G, MY, NY, U, and UOJ, visits to MER, MERC, MERF, MY, MYF, and VEN, photographic material available at Reflora-Virtual Herbarium (2022), the virtual herbaria of New York (NYBG-Steere Herbarium 2022), Paris (P Herbarium-Vascular Plants 2022), and Rio de Janeiro (JABOT 2022), plus photographic material from INPA, MA, PORT and UEC have been studied and identified. The type material was examined directly and/or through Jstor-Global Plants (2022). Samples were examined with a Leica MZ6 stereoscopic microscope, and the images of the specimens through measurement tools available in virtual sites or directly with the aid of a rule and comparing to the available scales. If there is more than one herbarium registration number, the most recent is chosen (for those with associated barcodes “bc” is added between herbarium acronym and herbarium registration number); for F, however, original registration number is maintained, since the number which is associated with a barcode is not visible in the specimens consulted. The term “*n.v.*” (*non visus*) is included for those duplicates that were not seen. Herbarium acronyms are cited according to Thiers (2022).

For the description of the new species, the criteria established by Grande (2018, 2019) are followed, including the differentiation of the different parts of the pistil, where the styloid corresponds to the styliform extension of the apex of the ovary (pseudostyle) plus the style itself. The interpretation of the glandular emergences of the foliar margins and of sepals as colleters, according to Thomas (1991). The inflorescences are solitary, although they are sometimes grouped into brachyblasts, and the axis includes a hypopodium (corresponding to the peduncle), a mesopodium and an epipodium, the latter two forming the pedicel and usually inconspicuous. The fruits are classified, according to the type of dehiscence, into subvalvular and circumcised. In some references, the subvalvular fruits are described as “indehiscent” or “irregularly dehiscent”, depending whether fruit opening is delayed or the valves cannot be clearly distinguished (*cf.*, Grande 2019; perhaps only *Ternstroemia washikiatii* really indehiscent —*cf.*, Cornejo and Ulloa 2016—). Leaves (more properly nomophylls) are usually of three types: those normally developed along main branchlets, those disposed in secondary minor branches (arising from the former), and reduced nomophylls (around floriferous sections of branchlets, alternating with hypsophylls). Only the normally developed nomophylls are included in the description. Colors are reported as found in dry material; for those structure with information on living material (according to herbarium labels), *in vivo* coloration is reported. Biogeographical areas follow the most recent system of Morrone (2017). The map (Fig. 3) was made with the aid of SimpleMapPR (Shorthouse 2010) and reflects coordinates as they appear in the herbarium labels (when expressed as a range plotted as an average), plus those that could be inferred with the aid of Google Earth (2022). The conservation status of the new species was determined according to the criteria of the

Red List of the International Union for Conservation of Nature (IUCN 2012), based on the information available in GeoCAT (Bachman et al. 2011) Google Earth and literature. Plant names and authors follows the International Plant Names Index (IPNI 2022).

RESULTS AND DISCUSSION

Ternstroemia dentata is a widespread species in northern South America. Three additional taxa, (viz., *T. laevigata*, *T. urophora* and an undescribed species from upper Río Negro and upper Orinoco rivers) are closely similar and have been mixed or misidentified. All of them have coriaceous larger leaves, more or less urceolate corollas, punctiform stigmata, 2 or 4-locular ovaries (when bilocular with two ovules in each cell, if tetralocular just one), and fruits more or less globose, ovoid or conical, with a conspicuous rostrum (at least $\frac{1}{2}$ the length of fruit body).

In the following paragraphs the new species is described, illustrated, and compared with most similar taxa. Further information on morphology, distribution, nomenclature and classification for the *Ternstroemia dentata* complex is available in Grande (2019, 2020 [2021]). A complete list of studied specimens is available in Appendix 1.

***Ternstroemia ostracophylla* J.R. Grande, sp. nov.** **TYPE: BRAZIL. Amazonas:** mun. Barcelos, platô da Serra Aracá, serra N, 6 h O do campo de pouso, 00° 51' N, 63° 22' W, 1150 m, 20 II 1984. *do Amaral* 1637 (Holotype: NY bc 1183331; isotype: RB bc 435987). Figs. 1, 2C, 3.

Arbuscula vel arbor parva *Ternstroemiam dentatam* aemulans, foliis percrassis, sepalis subaequalibus ac fructibus parvis tenuibusque (0.9–1 cm non 1,2–2 cm diam., pericarpio < 1 cm non 1–2.5 cm crasso) ab ea discrepat.

Shrub or small tree, 1–4 m tall, with erect or procumbent branches; **branchlets** (1–)2–5 per node. **Leaves** alternate or more or less grouped throughout branchlets (*i.e.*, pseudo-whorled); petioles 0.6–1.8 cm long; leaf blades 3.8–10 cm \times 1.9–5.7 cm, adaxially brown, abaxially ochraceous, sometimes greenish (and then also darker on the upper side), thickly coriaceous, elliptic, obovate-elliptic or (seldom) narrowly elliptic; base cuneate; margin slightly revolute and subentire towards base, discretely and widely toothed towards apex; apex discretely acuminate, sometimes obtuse or rounded, seldom emarginate (in reduced leaves); midvein impressed on the adaxial face and keeled on the abaxial surface, secondary venation obscure. **Inflorescences** solitary, axillar, spaced along branchlets or, more frequently, grouped in floriferous sections, where they are subtended by hypsophylls or reduced nomophylls; peduncles 0.6–2.3 cm long; hypsophylls early caducous, not seen; bracteoles deltoid to ovate, subopposite, keeled, the lower 0.6–0.7 \times 0.6–0.7 mm, upper ones *ca.* 1.1 \times 0.6 mm. **Flowers** hanging at anthesis; flower buds pinkish (*in vivo*); calyx greenish with pinkish or reddish tints (*in vivo*); sepals erect or patent, widely ovate, pointed at apex; outer sepals 0.5–0.6 \times 0.5 cm; inner sepals 0.5–0.7 \times 0.5 mm; corolla urceolate, whitish (*in vivo*) *ca.* 0.8 cm long, forming a tube *ca.* 0.4 mm long; sepals lobes triangular-ovate, membranaceous along margins. Androecium containing *ca.* 40 stamens *ca.* 5 mm long; filaments linear, *ca.* 2.5 mm long, with (*in vivo*); anthers oblong, *ca.* 2.5 mm long, yellow (*in vivo*), flattened dorsiventrally and with a conspicuous apicule *ca.* 0.7 mm long. Pistil *ca.* 1 cm long, scarcely exceeding the corolla; ovary ovoid, 4-locular, with a single ovule per locule, greenish (*in vivo*); stigma punctiform, bilobate. **Fruit** globose or subconic, 1.1–1.2 \times 0.9–1 cm, with the styloid concrecent, forming a rostrum of *ca.* 0.4 cm long, green when immature, yellow or orange at its maturation (including the persistent sepals and peduncle; *in vivo*); pericarp thin, <1 mm width. **Seeds** subreniform, laterally flattened, 6–7 \times 4 mm, 4 per fruit, bearing a red sarcotesta (*in vivo*).

Additional material (paratypes): BRAZIL. Amazonas: Barcelos. Serra do Aracá, Acampamento do fosso, Parque Estadual da Serra do Aracá, 19 IV 2014. *Barbosa-Silva* 263 (RB bc 873536); Barcelos. Serra do Aracá, trilha do acampamento do fosso para a cachoeira do Eldorado, passando pelo mirante, Parque

Estadual da Serra do Aracá, 20 IV 2014. *Barbosa-Silva* 282 (RB bc 873555); serra do Aracá, platô (ou encosta?), 200 km ao N de Barcelos, III 1984. *da Silva* 7170 (NY bc 1183447, NY bc 1279962); mun. Barcelos, platô da Serra Aracá, parte E da serra N, 00° 51' N, 63° 22' W, 1150–1250 m, 12 II 1994. *do Amaral* 1505 (NY bc 1183330); Barcelos. Parque Estadual da Serra do Aracá. Vegetação arbustiva com afloramentos e alagados, 29 IX 2011. *Forzza* 6556 (RB cb 715502); Barcelos. Parque Estadual da Serra do Aracá, 01 XI 2011. *Martinelli* 17284 (RB bc 686695); serra Aracá, 1000 m, 10 XII 1974. *Pires* 15038(59) (NY bc 1183393); plateau of N massif of serra Aracá, S side of N mountain, 00° 51–57' N, 63° 21–22' W, 1200 m, 12 II 1984. *Prance* 29006 (NY bc 1183385, RB bc 435937, U bc 283444); encosta da serra Aracá, 600 m, 31 I 1978. *Rosa* 2328 (NY bc 1183439); platô da serra Aracá, parte SE da serra N, 00° 51' N, 63° 22' W, 1150–1250 m, 24 II 1984. *Tavares* 138 (NY bc 1183454); Barcelos, Serra do Aracá, fase norte, topo da encosta, 00° 57' N, 63° 23' 30" W, 25 VIII 2001. *Vicentini* 1833 (INPA 214358); Barcelos, Serra do Aracá, face norte, topo da encosta, 00° 57' N, 63° 23' 30" W, 25 VIII 2001. *Vicentini* 1838 (INPA 214363). **COLOMBIA. Guainía:** Maimachi, serranía del Naquén, cerro Minas, alrededores del helipuerto-15 y camino hasta la cima del cerro, 01° 12' N, 68° 13' W, 900 m, 07 IV 1993. *Barbosa* 8330 (NY s.n.); mun. Maimachi, serranía de Naquén, cerca al helipuerto 15, 02° 13' N, 68° 14' W, 730 m, 30 VII 1992. *Cortés* 187 (NY s.n.), 188 (NY s.n.). **VENEZUELA. Amazonas:** dpto. Atabapo, macizo del Marahuaca, gran altiplanicie ubicada en el piedemonte SO del sector meridional del cerro Marahuaka ("Atahua-Shiho"), 03° 40' N, 65° 32' W, 950–1000 m, 14 XII 1992. *Huber* 13466 (MYF 14329).

Etymology: the specific epithet makes reference to the hardness and general aspect of leaves (φύλλον), similar when dry to a fragment of old pottery (οστρακον).

Habitat and distribution: *Ternstroemia ostracophylla* is found in the Guayana Shield, an ancient terrain of Precambrian origin encompassing eastern Colombia, southern Venezuela, northern Brazil and the Guianas (Guyana, Suriname and French Guiana). It has been collected in Brazil, Colombia and Venezuela, between 600 and 1250 m. It usually grows in shrublands on sandstone or white sand, less frequently in the nearby low forest (*Vicentini* 1833). *Ternstroemia dentata*, instead, usually thrives below 250 m, seldom reaching 400–500 m, 610 m in the Kanuku mountains, in savannas and transitional areas between forests and savannas, colonizing disturbed areas as *capoeiras* (burned, felled, or plowed places for subsistence agriculture) and roadsides. From a biogeographical point of view, species of the *Ternstroemia dentata* complex should be included in the Boreal Brazilian and South Brazilian dominia. The new species, like *Ternstroemia urophora*, is found in the Imerí province, in contrast to *T. laevigata*, which is confined to the Guayana province. *Ternstroemia dentata*, on the other hand, is distributed over a wider area, throughout the provinces of Guayana, Guayana Lowlands, Roraima, Madeira and Rondônia; although it does not overlap in its distribution area with those species, it becomes a neighbor of one of them (viz., *T. laevigata*; cf., Fig. 3). *Ternstroemia dentata* and *T. urophora* are more or less common species in lower Río Negro, but while *T. dentata* occupies the interfluvial space ("terra firme"), *T. urophora* is found on banks of black water rivers (*igapós*) and the nearby ecosystems on wet sand (*campinas*). Bittrich et al. (1993) cited *Ternstroemia laevigata* for that area, but after the revision of Grande (2019) it has been established that it has only been found in the upper basins of the Branco and Caroní rivers (Venezuela and Brazil). The populations from the vicinity of Manaus, cited by Bittrich et al. (1993) as of this species, correspond to *T. urophora* (Grande 2019, 2020 [2021]).

Conservation: according to the criteria of the IUCN Red List (IUCN, 2012) the new species is not endangered ("Least Concern" or LC). Extent of occurrence (89,008 km²) is large enough and localities where the species grows are either legally protected or well preserved. According to area of occupancy (16,000 km²) it could be Vulnerable (VU), but just point B1a matches. Low number of localities is probably an artifact since the area where the species grows is still poorly sampled.

Affinities: similar to *Ternstroemia dentata*, with which it shares broad and coarsely toothed leaves. That species, however, tends to have obovate blades, conspicuous teeth relatively distant from each other,

faint (but obvious) secondary venation, inner sepals with truncate to rounded apex, clearly lighter than the outer ones, and yellowish-ochraceous with a spot or macule along midvein, which is notably developed towards the base (Grande 2019). *Ternstroemia laevigata* and *T. urophora* are the other two most similar species. Both of them, however, have more or less concolorous leaves with sub-entire margins. *Ternstroemia urophora* may also be differentiated by the subequal or gradually larger (from outside to inside) sepals and *T. laevigata* by the unequal sepals and reddish coloration (for additional differences between these four species, see Table 1). Grande 2020 [2021] erroneously cites the sepals of *Ternstroemia laevigata* as subequal, but they are, actually, of two different types (as in *T. dentata*). *Ternstroemia caput-medusae* and *T. rupestris* seems to be also related, but they can be readily distinguished by the complex inflorescences (*cf.*, Grande 2020 [2021]). Some specimens of *T. urophora* (especially Nelson P21090; Appendix 1) show very dense floriferous areas on branchlets, but further development apparently elongates internodes and produces additional normally developed nomophylls.

Ternstroemia ostracophylla was not considered by Boom (1989), who describes three new species from Serra do Aracá and its surroundings (where the species has been more often collected). Thence, several collections have been determined either as *T. dentata* (usually *incertae sedis*) or *T. sp. indet.* Previously available identifications include “*Ternstroemia dentata*” (det. B.M. Boom in *Prance* 29006 [U!], 1989), “*Ternstroemia cf. dentata*” (anonymous det. in *do Amaral* 1505 [NY!]), “*Ternstroemia aff. dentata*” (det. M. Córdoba and R. Cortés in *Cortés* 187 [NY!] and 188 [NY!]) and “*Ternstroemia sp. nov.?*” (det. J.R. Grande in *Huber* 13466 [MYF!]). More recently, it has been determined in RB (!) as “*Ternstroemia tepuiensis*” (*Martinelli* 17284, *Prance* 29006, *do Amaral* 1637, *Forzza* 6556, *Barbosa-Silva* 263 and 282, det. G.S. Barbosa-Silva). The last species, however, is notably different and is related, instead, to *Ternstroemia carnosa* Cambess., *T. circumscissilis* Kobuski, *T. crassifolia* Benth., *T. discoidea* Gleason, *T. distyla* Kobuski, and *T. unilocularis* Kobuski & Steyerm., whose fruits are circumcisely dehiscent (*cf.* Grande, 2018, 2019, 2020 [2021]).

Key to the species of the *Ternstroemia dentata* complex

- 1a. Inner sepals conspicuously larger and/or wider than outers, discolored, apically rounded 2
 1b. Sepals subequal or gradually becoming smaller from outside to inside, concolorous; apex of inner sepals pointed 3
- 2a. Leaf blades conspicuously toothed, obovate, elliptic-obovate or obovate-lanceolate, acuminate or rounded at apex (seldom retuse), usually ochraceous; inner sepals ochraceous to yellowish towards margins and brownish towards base and along midvein *T. dentata* (Aubl.) Sw.
 2b. Leaf blades subentire, elliptic to elliptic-obovate, apically obtuse, rounded or, seldom, subacute, ochraceous or reddish-ochraceous; inner sepals reddish-ochraceous towards margins and reddish-brown towards center and along midvein *T. laevigata* Wawra
- 3a. Leaf blades subentire or coarsely and inconspicuously serrate-dentate, coriaceous, generally ochraceous, brownish to dark brown when dry, concolorous, with secondary venation (usually) forming an angle of 45°–60° to midvein, conspicuous or not *T. urophora* Kobuski
 3b. Leaf blades conspicuously and widely toothed, thickly coriaceous, usually brownish in the upper side and ochraceous abaxially, sometimes greenish (and then –also– conspicuously darker by the upper side); secondary venation forming an angle of *ca.* 45° to midvein *T. ostracophylla* J.R. Grande

Table 1. Comparative morphology of the species from the *Ternstroemia dentata* complex (*T. dentata* (Aubl.) Sw., *T. laevigata* Wawra, *T. ostracophylla* J.R. Grande and *T. urophora* Kobuski).

	<i>T. dentata</i>	<i>T. laevigata</i>	<i>T. ostracophylla</i>	<i>T. urophora</i>
Number of branchlets per node	1–2(3–5)	1–3	(1–)2–5	1–2(3–4)
Petiole length	1–2 cm	0.9–1.8 cm	0.6–1.8 cm	(0.4–1)1.3–2.5 cm
Leaf blade texture	coriaceous	coriaceous	thickly coriaceous	coriaceous
Leaf blade shape	ovate, obovate-elliptic or obovate-lanceolate	ovate or obovate-elliptic	elliptic, obovate-elliptic or (seldom) narrowly elliptic	elliptic or obovate-elliptic
Leaf blade margin	coarsely and remotely toothed (seldom subentire)	subentire	slightly revolute and subentire towards base, discretely and remotely toothed towards apex	subentire to finely and discretely toothed
Leaf blade apex	acuminate, rounded or, seldom, retuse	rounded to discretely acuminate	discretely acuminate, sometimes obtuse or rounded, seldom emarginate (in reduced leaves)	acuminate to caudate
Secondary venation (to midvein)	ca. 45°	ca. 45°	ca. 45°	45°–60°
Leaf blade coloration (<i>in sicco</i>)	ochraceous to reddish-ochraceous, seldom greenish	reddish-ochraceous, seldom greenish	adaxially brown, abaxially ochraceous, sometimes greenish (and then also darker adaxially)	ochraceous, brown or dark brown, seldom slightly purple (especially in lower side) or adaxially greenish
Peduncle length	0.7–1.2 cm	ca. 2 cm	(0.1–)0.6–2.3 cm	(0.1–)0.6–1.7
Sepals	dimorphic, inner sepals noticeably larger, discolored; the apex rounded	dimorphic, inner sepals noticeably larger, discolored; the apex rounded	subequal, gradually smaller from outside to inside, concolorous; the apex pointed	subequal, gradually smaller from outside to inside, concolorous; the apex pointed
Sepal apex	rounded	rounded	pointed	pointed
Outer sepal length	5–6 mm	ca. 6 mm	(4.5–)5–6 mm	ca. 5 mm
Outer sepal coloration (<i>in sicco</i>)	Brown	reddish-brown	ochraceous	reddish-ochraceous to dark brown
Inner sepal length	7–9 mm	8–9 mm	5–7 cm	5–7 cm
Inner sepal coloration (<i>in sicco</i>)	ochraceous to yellowish, with a central brown spot	reddish-ochraceous, with a central reddish-brown spot	ochraceous	reddish-ochraceous to dark brown
Corolla tube relative length	1/2	1/2	1/2	1/3
Fruit shape	globose, ovoid or subconic	ellipsoid to ovoid	globose or subconic	globose, ovoid or conic
Fruit size (excluding rostrum)	1.4–1.7 × 1.2–2 cm	ca. 1.6 × 1.4 cm	1.1–1.2 × 0.9–1 cm	1.4–3 × 1.3–2.3 cm
Pericarp thickness	1–2.5 mm	ca. 1 mm	< 1 mm	< 1 mm

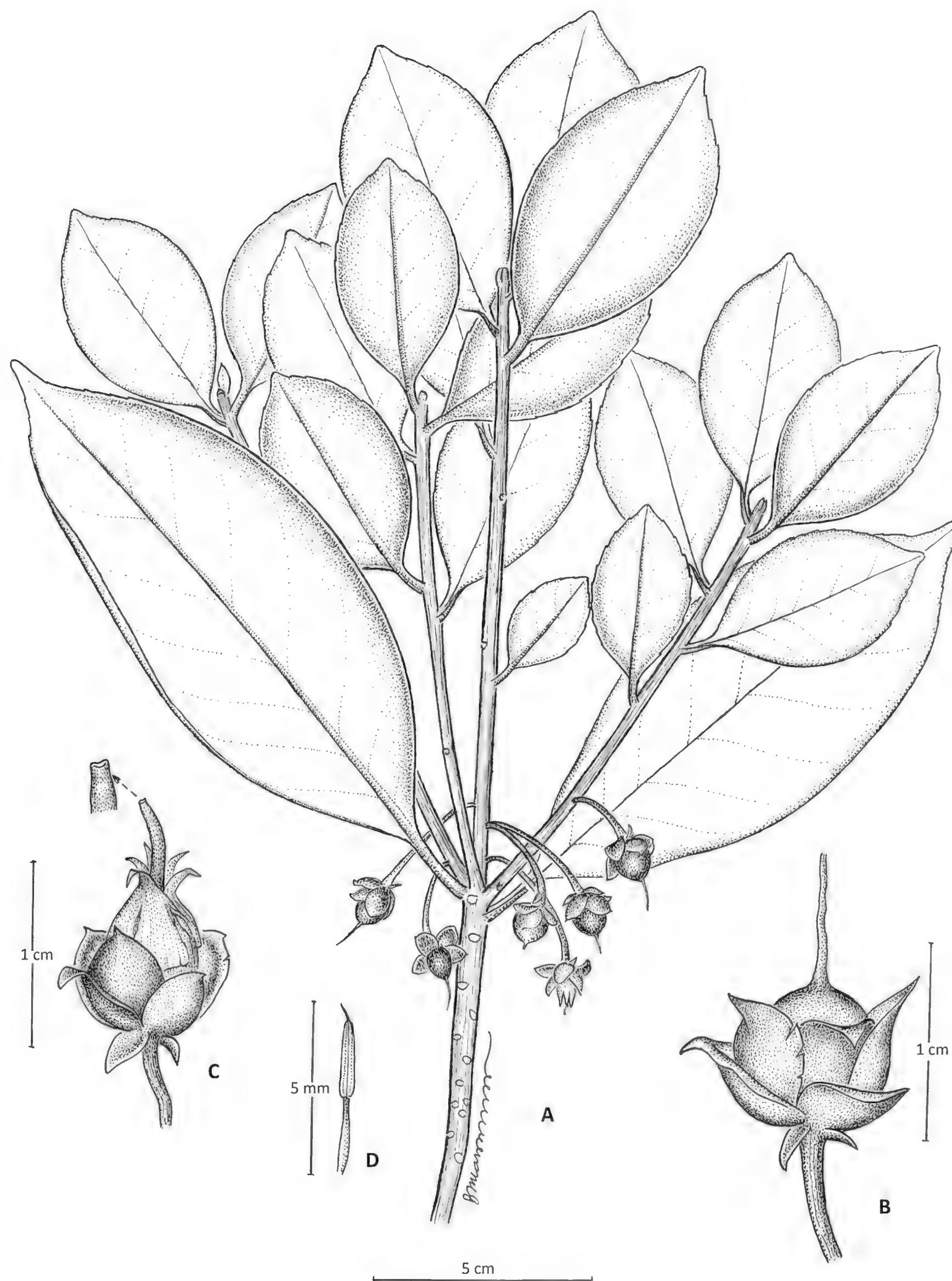


Figure 1. Line-drawing of *Ternstroemia ostracophylla* J.R. Grande, sp. nov. A. Habit, showing a flower, immature and submature fruits. B. Submature fruit. C. Immature fruit, with corolla still attached; detail of stigma (magnified). D. Stamen. A–B from holotype (*do Amaral 1637* [NY bc 1183331]); B–D from Prance 29006 (U bc 283444).



Figure 2. Species from the *Ternstroemia dentata* complex: A. *T. dentata* (Aubl.) Sw. (Maguire 24685 [NY 927187]). B. *T. laevigata* Wawra (Maguire 40280 [NY 1183469]). C. *T. ostracophylla* J.R. Grande, sp. nov. (Prance 29006 [NY 1183385]). D. *T. urophora* Kobuski (Prance 18055 [NY 1183381]).

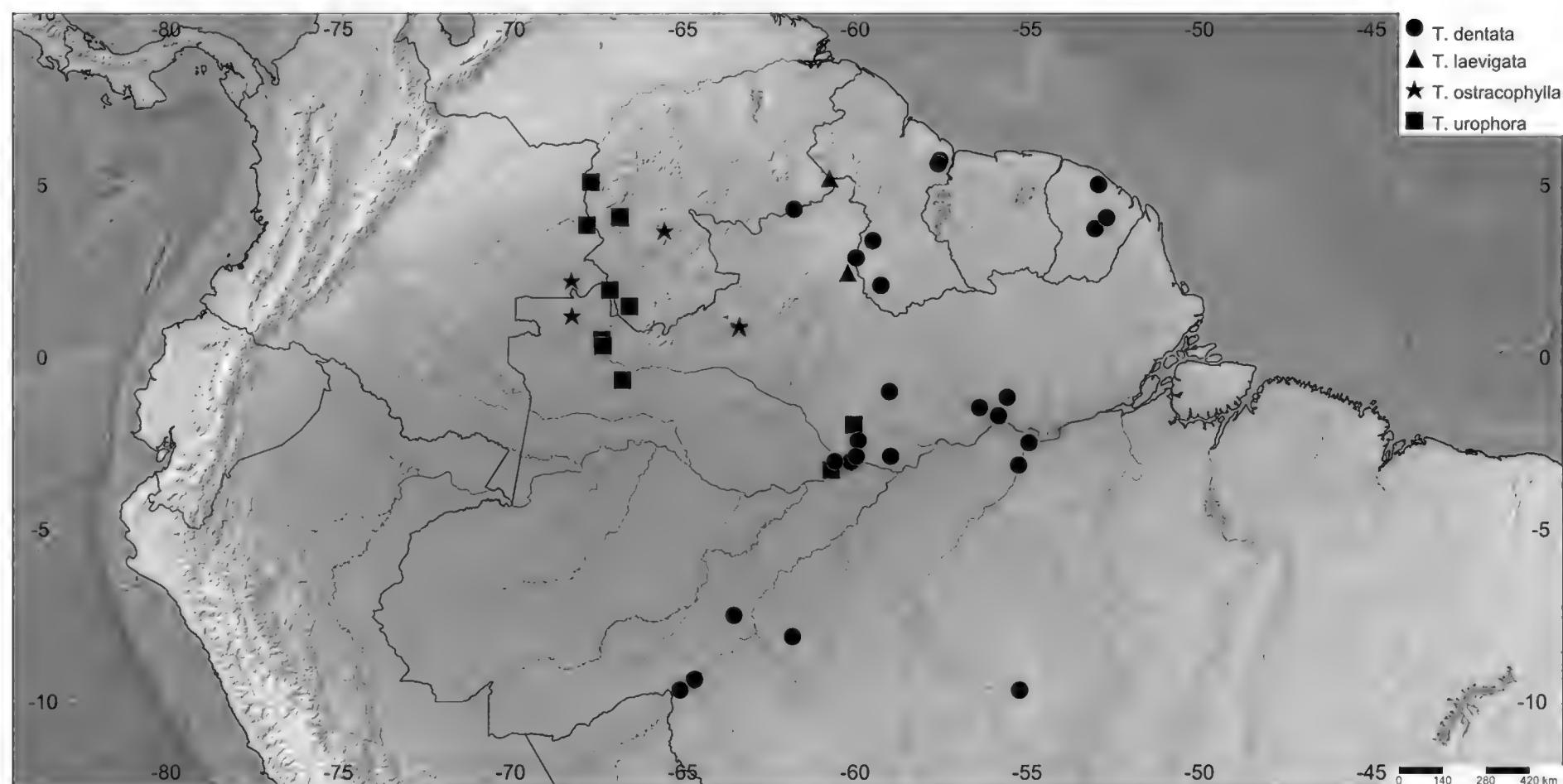


Figure 3. Distribution map of *Ternstroemia dentata* (Aubl.) Sw., *Ternstroemia laevigata* Wawra, *T. ostracophylla* J.R. Grande, sp. nov., and *T. urophora* Kobuski.

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Appendix 1. Voucher specimens included in map (excluding those of *Ternstroemia ostracophylla* J.R. Grande, *sp. nov.*, which are cited in text).

- Ternstroemia dentata* (Aubl.) Sw., Prodr. [O. P. Swartz] 81. 1788, *non* Spreng. ex DC., *nom. illeg.*, Mém. Soc. Phys. Genève 1: 411. 1821. *Taonabo dentata* Aubl., Hist. Pl. Guiane 1: 569, 4: tab. 227. 1775. *Ternstroemia dentata* var. *typica* Wawra, Fl. Bras. (Martius) 12(1): 279. 1886, *nom. inval.* *Mokof dentata* (Aubl.) Kuntze, Revis. Gen. Pl. 1: 63. 1891, *sub* *Mokofua dentata* (Aubl.) Kuntze. LECTOTYPE (designated by Vieira et al. 2021): [FRENCH GUIANA]: Habitat in sylvis supra montem Serpent dictum, “Guyane”, *s.d.*, *Aublet s.n.* (BM bc 41973; isolectotype: S bc 1115324).
- Ternstroemia dentata* var. *α. multiflora* Choisy, Mem. Soc. Phys. Hist. Nat. Genève 14: 106. 1855. *Ternstroemia multiflora* Spruce ex Choisy, *ibid.*, *nom. nud.* LECTOTYPE (designated by Grande 2020 [2021]): BRAZIL. Pará: in vicinibus Santarem, 09/1850, *Spruce s.n.* (F 686545; isolectotype: BM bc 41938, E bc 296781, FI bc 6035, G bc 366238, G bc 366274, GH bc 306606, K bc 687881, NY bc 1239903, NY bc 1239904, P bc 780884).
- Ternstroemia dentata* var. *γ. oblongifolia* Choisy, Mem. Soc. Phys. Hist. Nat. Genève 14: 106. 1855. *Ternstroemia dentata* var. *α. opaca* Wawra, Fl. Bras. (Martius) 12(1): 279. 1886. LECTOTYPE (designated by Vieira et al. 2021): BRAZIL. Amazonas: in sylvis primaevis ad Ega [presently Tefé], 1831, Poeppig 2667 (F 875286; isolectotype: F 686248, G bc 366278, HAL bc 77007, NY bc 1239923).
- Ternstroemia dentata* var. *β. latifolia* Wawra, Fl. Bras. (Martius) 12(1): 279. 1886. LECTOTYPE (designated by Grande 2020 [2021]): BRAZIL. Amazonas: in vicinibus Barra, *Spruce 1045* (NY bc 127665; isolectotype: M bc 165337).
- Ternstroemia megaphylla* J.A. Vieira & D. Sampaio, Neodiversity 14: 8, figs. 2–3. TYPE: BRAZIL. Amapá: mun. Macapá, 7 km NW of Riozinho on highway Perimetral Norte (BR210), *ca.* 01°21' N, 53°15' O, 31 XII 1984, *Rabelo 3120* (holotype: NY bc 1183432; isotype: HAMAB *n.v.*, US 3433327 *n.v.*).

Additional material: BOLIVIA. La Paz: prov. Iturralde, Luisita, O del río Beni, zona inundada del río Muqui, 13° 05' S, 67° 15' W, 180 m, 1 III 1984, *Beck 10149* (NY *s.n.*). **BRASIL. Amapá:** estrada até Matapi, atrás Porto Grande, 17 X 1979, *Austin 7068* (NY bc 1183315, UEC 21137); mun. Macapá, 7 km NW of Riozinho on highway Perimetral Norte (BR210), *ca.* 01° 21' N, 53° 15' W, 31 XII 1984, *Rabelo 3120* (NY cb 1183432); 02 IV 1982, *Rosa 4126* (NY bc 1183438). **Amazonas:** Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, 02° 53' N, 59° 58' W, 10 VIII 1995, Assunção 213 (UEC 11311, VEN 298791); estrada Manaus-Itacoatiara km 9, 2 III 1956, *Coêlho s.n.* (NY *s.n.*); mun. Tefé, rio Solimões, margem direita, lago Tefé, Vila Nogueira, 12 X 1982, *do Amaral 23* (NY bc 1183327); Manáos, estrada do Paredão, 8 IV 1943, *Ducke 1216* (NY bc 1183324); Tarumã Grande, 1 km N from the junction of rio Negro and igarape Tarumã, 03° 02' S, 60° 08' W, 23 XI 1977, *Keel 307* (NY *s.n.*, NY bc 1183414); basin of rio Madeira, Mun. Humayta, *pr.* Livramento, on rio Livramento, 12 X–6 XI 1934, *Krukoff 6779* (B bc 10 0423788, G bc 374638, G bc 374638, NY *s.n.*, U bc 283440); basin of rio Madeira, mun. Humayta, on plateau between rio Livramento and rio Irixuna, 7–18 XI 1934, *Krukoff 7087* (B bc 10 0423789, G bc 374585, G bc 374585, NY *s.n.*, U bc 283441); basin of rio Madeira, mun. Humayta, on plateau between rio Livramento and rio Irixuna, 7–18 XI 1934, *Krukoff 7287* (NY *s.n.*); mun. Manaos, along road to Aleixo, 12 VIII–1 IX 1936, *Krukoff 8036* (G bc 374589, NY *s.n.*); rio Negro, margem direita, 50 km acima de Manaus,

Campo Amélia (fazenda Belo Horizonte), 03° 02' S, 60° 35' W, 18–19 VIII 1985, *Nelson* 1422 (MYF 12365, NY bc 1183422); dtto. Agropecuário, fazenda Porto Alegre, Reserva 3402 (Cabo Frio) of the WWF/INPA MCS project, 02° 25' 25" S, 59° 54' 38" W, 50–150 m, 21 I 1989, *Pacheco* 121 (NY s.n., U bc 283443); estrada da Reserva Florestal Ducke, capoeira aberta de terra firme, solo arenoso, 19 III 1958, *Pessoal do C.P.F.* s.n. (NY bc 1183427); Ega (=Tefé), 1832, *Poeppig* 2667 (NY bc 1239923); km 8, colônia Santa Antonio, 08 IX 1966, *Prance* 2221 (G bc 374639, G bc 374639, NY s.n., U bc 283442); Campo Amélia (fazenda Belo Horizonte), entre igarapé Acajatuba e margem direita do rio Negro, 03° 02' S, 60° 35' W, 21 IV 1986, *Prance* 30041 (MYF 12595, NY bc 1183375); Manaus, SW corner of Ducke Forest Reserve, 14 km of INPA by road via Bairro de São José, 17 IX 1987, *Pruski* 3272 (NY bc 1183431, VEN 401835); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, área do Projeto Copaiba, 02° 53' S, 59° 58' W, 26 IV 1988, *Ramos* 1866 (U bc 61873); estrada Manaus-Itacoatiara, km 28, 22 XI 1960, *Rodrigues* 1922 (NY bc 1183402); estrada Manaus-Boa Vista, km 10, 24 X 1961, *Rodrigues* 2099 (NY bc 1183403); igarapé do Matrinchão, 12 IV 1961, *Rodrigues* 2350 (NY bc 1183404); Manaus, igarapé do Buião, 24 IV 1963, *Rodrigues* 5053 (NY bc 1183407); mun. São Gabriel da Cachoeira, alto rio Negro, próximo à boca do igarapé Tuari; lago Amaro, do lado oposto à ilha de Aparecida, 00° 20' N, 67° 19' W, 06 XI 1987, *Rodrigues* 10867 (NY bc 1183413); rio Jarí, monte Dourado, planalto A, 04 X 1968, *Silva* 1107 (NY bc 1183450); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, próximo a entrada da reserva, 02° 53' S, 59° 58' W, 13 II 1995, *Sothers* 325 (G bc 374637, UEC 111444); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, estrada de acesso ao alojamento, 02° 53' S, 58° 58' W, 13 XII 1995, *Sothers* 710 (VEN 354226); pr. Barra, prov. Rio Negro, XII–III 1850–1, *Spruce* 1045 (NY bc 127665, [NY 19553 (photo ex M)], [G bc 374588], [G bc 374719], [G bc 374720]); pr. Barra, prov. Rio Negro, V 1851, *Spruce* 1302 (NY bc 1183542); INPA, estrada do Aleixo, km 3, Manaus, near tracking station; 26 XII 1973, *Steward P* 20130 (NY s.n.); [prov.] Rio Negro, Manáos, VII 1900, *Ule* 5166 (G bc 374590); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, Igarapé do Acará, na trilha da divisa, 02° 53' S, 59° 58' W, 23 V 1995, *Vicentini* 965 (G bc 374591, U bc 20610); rodovia do Estanho, margem da rodovia a 12 km de Humaitá, 08° 07' S, 61° 49' W, 25 II 1979, *Vieira* 164 (NY bc 1183457); road Humaitá to Lábrea, 63 km W of Humaitá, 07° 30' S, 63° 31' W, 30 IX 1979, *Zarucchi* 2607 (NY bc 1183460). Mato Grosso: mun. Novo Mundo, Parque Estadual Cristalino, serra de Rochedo, acesso pela fazenda AJJ, 09° 40' 23" S, 55° 13' 40,71" W, 19 VIII 2008, *Sasaki* 2244 (NY bc 1146409). **Pará:** mun. Oriximiná, rio Trombetas, margem direita ao N da mineração Sta. Patricia, 11 VII 1980, *Cid Ferreira* 1458 (NY bc 1280882, NY bc 1183357); mun. Oriximiná, estrada Oriximiná-Óbidos km 12, margem esquerda, 14 IX 1980, *Cid Ferreira* 2494 (NY bc 1183352); mun. Oriximiná, área da mineração Rio Norte, 5 km da vila residencial, 01° 28' S, 56° 23' W, 11 XI 1987, *Cid Ferreira* 9558 (NY bc 1183349); mun. Óbidos, 91 km de Oriximiná nos campos de Ariramba, entre rio Jaramacaru e igarapé Mutum, 01° 10' S, 55° 35' W, 4 XII 1987, *Cid Ferreira* 9751 (NY bc 1183350); mun. Óbidos, campos do Ariramba no lugar Tabuleta, 18 km do rio Jaramacaru, 01° 10' S, 55° 35' W, 6 XII 1987, *Cid Ferreira* 9794 (NY s.n.); mun. Oriximiná, 10 km de Oriximiná na estrada p/ Óbidos (PA-28), 01° 42' S, 55° 50' W, 10 XII 1987, *Cid Ferreira* 9826 (NY bc 1183347); mun. Oriximiná, 10 km de Oriximiná na estrada p/ Óbidos (PA-28), 01° 42' S, 55° 50' W, 10 XII 1987, *Cid Ferreira* 9828 (NY bc 1183346); mun. Óbidos, campos de Ariramba, campos entre o igarapé do Mutum e rio Ariramba, 4 XII 1987, *Farney* 2067 (NY s.n.); Marabá, Carajás, serra norte, estrada do N-1, 29 km do acampamento, 7 VIII 1982, *Maciel* 790 (NY bc 1183416); mun. Almeirim, monte Dourado, estrada do Parú, próximo à entrada da torre 8, 17 X 1985, *Pires* 665 (NY s.n.); Almeirim, mount Dourado, área da Agua Azul, próximo à gleba Angelim da Reserva Genética, 17 IX 1986, *Pires* 1379 (NY bc 1183430, NY bc 1279957); BR 163, Cuiabá-Santarem highway; northern foothills of serra do Cachimbo, 11 XI 1977, *Prance* 25195 (NY bc 1183368); mun. Santarém, peninsula em frente a Alter do Chão, 02° 29' S, 54° 57' W, 22 IV 1989, *Sanaiotti* 18 (NY bc 1183442); pr. Santarém, prov. Pará, IX 1850, *Spruce* 1083 (NY bc 1239904, [NY bc 1239903], [NY 21486 (photo ex C)]); Santarém, subida da serra Piroca, 15 XII 1978, *Vilhena* 330 (NY s.n.). **Rondônia:** km 5 da rodovia Vilhena-Porto Velho, 03 I 1979, *Silva* 4111 (NY s.n.); chapada dos Parecis, a 29 km de Vilhena, 12° 45' S, 60° 10' W, 28 X 1979, *Vieira* 739 (NY bc 1183458); rodovia RO-399, a 13 km de Vilhena, km 20, base da chapada dos Parecis, 12° 45' S, 60° 10' W, 03 XI 1979, *Vieira* 887 (NY bc 1183456). **FRENCH GUIANA:** pic Matécho, versant S, 03° 44' N, 53° 02' W, 450 m, 19 IX 2000, *de Granville* 14281 (NY s.n., U bc 64758); Camopi?, Haut Oyapock, sommet O du mont St. Marcel, 450 m, 26 VII 1975, *de Granville* 2566 (B bc 10 0423800, NY s.n., U bc 283397); montagnes des Nouragues, bassin de l'Approuague, Arataye, 04° 03' N, 52° 42' W, 410 m, X 1989, *Larpin* 668 (U bc 245881); Réserve des Nouragues, Station de Recherches, inselberg, 04° 03' N, 52° 42' W, 410 m, 7 III 2004, *Poncy* 1820 (U bc 228201); Crique Plomb, 05° 01' N, 52° 55' 40" W, 110 m, 23 X 2002, *Prévost* 4654 (B bc 10 0141863); route Charvein Acarounay, km 6600, 20 I 1955, *Sabatier* 4785 (B bc 10 0141865, NY bc 927186); Acarouany, 1856, *Sagot* 60 (U bc 283456); montagnes des Nouragues, bassin de l'Arataye, sommet, 04° 03' N, 52° 42' W, 18 II 1988, *Sarthou* 212 (NY s.n.). **GUYANA:** Wabuwak, Kanuku mountains, 609.6 m, XI 1948, *Fanshawe?* (Forest Department of British Guiana) WB 424/5821 (NY bc 927185); Wabuwak, Kanuku mountains, 609.6 m, XI 1948, *Fanshawe?* (Forest Department of British Guiana) WB 474/5883 (NY bc 927184); Rupununi savanna, Mora savanna, pr. Toroebroe creek, 03° 23' N, 59° 29' W, 145 m, 19 XI 1987, *Jansen-Jacobs* 1037 (B bc 10 0423796, NY bc 927188, U bc 223342); Gunn's, Essequibo river, 240–260 m, 3 IX 1989, *Jansen-Jacobs* 1430 (B bc 10 0423790, NY bc 927189, U bc 223341); Rupununi Kuyuwini landing, Kuyuwini river, 02° 05' N, 59° 15' W, 150–250 m, 28 IX 1992, *Jansen-Jacobs* 3139 (NY bc 927182); East Berbice-Corentyne, S Awara savanna, 56.33 km S of Torani canal, on Canje river, 4.83 km SE of Digitima creek, 05° 43' N, 57° 32' W, 1–25 m, 18 XII 1986, *Pipoly* 9340 (NY s.n.); East Berbice-Corentyne, W bank of Canje river, Cow savanna, ca. 1 km N of Digitima creek, 05° 37' N, 57° 35' W, 0–20 m, 14 IV 1987, *Pipoly* 11564 (NY s.n., [VEN] s.n.); East Berbice-Corentyne, W bank of Canje river, Cow savanna, ca. 1 km N of Digitima creek, 1–20 m, 14 IV 1987, *Pipoly* 11566 (NY s.n.); East Berbice-Corentyne, W bank of Canje river, Cow savanna, ca. 1 km N of Digitima creek, 05° 37' N, 57° 35' W, 0–20, 14 IV 1987, *Pipoly* 11571 (NY s.n., [VEN] s.n.); East Berbice-Corentyne, W bank of Canje river, Cow savanna, ca. 1 km N of Digitima creek, 1–20 m, 14 IV 1987, *Pipoly* 11581 (NY s.n., [VEN] s.n.). **SURINAM:** Sectie O, 28 I 1906, *Gongrijp* 64 (U bc 2834--, U bc 283458); pr. Jodensavanne (fluv. Suriname), 24 V 1957, *Heyligers* 500 (U bc 283453); pr. Jodensavanne (fluv. Suriname), 30 X 1956, *Heyligers* 503 (U bc 283454); pr. Jodensavanne (fluv. Suriname), 17 XII 1956, *Heyligers* 529 (U bc 283445); pr. Jodensavanne (fluv. Suriname), 17 XII 1956, *Heyligers* 529 (U bc 283445); pr. Jodensavanne (fluv. Suriname), 17 XII 1956, *Heyligers* 529 (U bc 283445).

Suriname), 18 I 1957, *Heyligers* 570 (U bc 283446); pr. Jodensavanne (fluv. Suriname), 30 I 1957, *Heyligers* 594 (U bc 283447); pr. Jodensavanne (fluv. Suriname), 17 VI 1957, *Heyligers* 826 (U bc 283449); pr. Jodensavanne (fluv. Suriname), 18 VI 1957, *Heyligers* 828 (U bc 283450); Saramacca, Kappel savanna, prope pedem australem montis Tafelberg, 300 m, 20 II 1961, *Kramer* 3295 (U bc 283451); Tafelberg ("Table Mountain"), 485 m, 10 IX 1944, *Maguire* 24685 (NY bc 927187); Tafelberg ("Table Mountain"), 485 m, 10 IX 1944, *Maguire* 24685 (U bc 223343, VEN 39289); Sipaliwini savanna area on brazilian frontier, "4-Gebroeders" mountains, 450 m, 18 X 1968, *Oldenburger* 307 (U bc 283452); Sipaliwini savanna area on brazilian frontier, "camp-forest" on W slope of "4-Gebroeders" mountains, 365 m, 30 XI 1968, *Oldenburger* 587 (NY s.n., U bc 223340); Zanderij I, X 1944, *Stahel* 240 (B bc 10 0423791, NY s.n., U bc 223295); achter Zanderij I, 02 III 1959, *van Donselaar* 467 (U bc 283459); Coesewijne-savanna, opname 282, 16 III 1959, *van Donselaar* 655 (U bc 283460); dtto. Brokopondo, 8 km ESE of village Browns weg, afterwards lake, 16 X 1964, *van Donselaar* 1690 (U bc 283461); Brinckhill (Saban Pasi) Nature Reserve, 17 X 1967, *Wildschut* 11832 (NY s.n.); Nature Reserve Brinckheuvel, Saban Pasi savanne, 17 X 1967, *Wildschut* 11832 (U bc 223294). **VENEZUELA: Bolívar:** dtto. Piar, Zapata, a 10 km al SO de Icabarú, 500 m, 12 II 1986, *Susach* 1105 (NY s.n., PORT 18748).

Ternstroemia laevigata Wawra, Fl. Bras. (Martius) 12(1): 281, tab. 55. 1886. *Moko laevigata* (Wawra) Kuntze, Revis. Gen. Pl. 1: 63. 1891. **LECTOTYPE (designated by Grande 2020 [2021]):** **VENEZUELA:** Roraima, *R.H. Schomburgk* 573 (K bc 697496; isolectotypes: BM bc 41988, BM bc 41989, F 869787, F 686522, G bc 366231, G bc 366277, NY bc 127655, P bc 780876, P bc 780877).

Additional material: BRAZIL: Roraima: 8.05 km E of serra Sabana, 720 m, 16–18 XII 1954, *Maguire* 40280 (NY bc 1183469); summit of serra da Lua, 02° 25–29' N, 60° 11–14' W, 1400 m, 24 I 1969, *Prance* 9440 (NY bc 1183365). **VENEZUELA:** Roraima, *Schomburgk* 573 (F 686522, F 869787, G bc 366231, K bc 697496, NY bc 127655).

Ternstroemia urophora Kobuski, J. Arnold Arbor. 32(2): 153. 1951. **TYPE: BRAZIL. Amazonas:** Manáus, Rio Tarumá-mirí, matinha marginal d'una campina arenosa, 17 VII 1943, *Ducke* 1288 (holotype: A bc 306658; fragment: A 25053; isotypes: NY bc 1239901, US bc 409624).

Additional material: BRAZIL. Amazonas: along Rio Marié, at Marauná, 00° 40' S, 66° 45' W, 06 VI 1979, Alencar 470 (NY bc 1183314); Manaus-Caracarai road, km 140, 27 IX 1973, *Berg* P18171 (NY s.n., NY bc 1183318); Manaus-Caracarai road, pr. km 130, 13 XI 1973, *Berg* P19546 (NY bc 1183317); mun. São Gabriel da Cachoeira, upper rio Negro, rio Cubate, tributary of rio Içana, 30 min. by motorboat sup. mouth, 03 XI 1987, *Daly* 5563 (NY bc 1183319); pr. Manaus, igapó of Tarumá-mirim, ca. 20 min. per motorboat sup. rio Negro, 28 VIII 1991, *do Amaral* 91/92 (NY bc 1183328); mun. Novo Japurá, rio Japurá, margem direita, lago do Mapari, 11 XI 1982, *do Amaral* 433 (NY cb 1183329); Manáos, rio Tarumá-miry, 04 VII 1941, *Ducke* 1212 (NY bc 1183325); mun. Presidente Figueiredo, "Campina das Pedras", ubicada en el km 115 de la rodovia BR-174 (Manaus-Caracarai), en el lado oriental del igarapé das Lajes, 01° 58' S, 60° 02' W, 100 m, 29–30 VI 1985, *Huber* 10683 (NY bc 1183360); boca do rio Içana, local chamado Boa Vista (antigo Grilo), 00° 30' N, 67° 21' W, 12 XI 1987, *Kawasaki* 118 (NY s.n.); basin of rio Solimoes, Tonantins, 03 VIII 1941, *Krukoff* 12173/84 (NY bc 1183335); rio Negro, at Porto Camanaus, 19 X 1978, *Madison* 6486 (NY bc 1183417); Manaus-Caracarai road, km 130, igarapé Lages, 10 V 1974, *Nelson* P21090 (NY bc 1183423); rio Cuieiras, 50 km upstream, 1 IV 1974, *Ongley* P21776 (NY bc 1183425); 2 km from rio Cuieiras at 2 km inf. mouth of rio Brancinho, 14 IX 1973, *Prance* 17906 (NY bc 1183370, U bc 283510); rio Cuieiras, pr. Jarada, 17 IX 1973, *Prance* 18055 (NY bc 1183381); Manaus-Caracarai road, km 130, igarapé Lages, 20 VI 1974, *Prance* 21144 (NY bc 1183380); Manaus-Caracarai road, km 130, igarapé Lages, 20 VI 1974, *Prance* 21144 (NY bc 1183380); Manaus-Caracarai road, km 130, igarapé Lages, 31 VIII 1974, *Prance* 21693 (NY bc 1183373); rio Cuieras, sup. mouth of rio Brancinho, 11 IX 1973, *Prance* P17712 (NY bc 1183382); mun. São Gabriel da Cachoeira, alto rio Negro, próximo a boca do igarapé Tuari, lago Amaro, do lado oposto à ilha de Aparecida, 00° 20' N, 67° 19' W, 06 XI 1987, *Rodrigues* 10867 (NY bc 1183413); rio Cuieras, Tucunaré, margem direita, pouco abaixo do Repartimento, 16 IX 1964, *Rodrigues* 6056 (NY bc 1183409). **COLOMBIA. Guainía:** ca. 5 km N of Boca de Casiquiare (where Negro, Guainía and Casiquiare rivers join), S side of caño, 01° 57' N, 67° 07' W, 120 m, 05 II 1980, *Liesner* 9075 (NY s.n.). **VENEZUELA. Amazonas:** depto. Casiquiare, ca. 20 km al SE de San Fernando de Atabapo, 03° 50' N, 67° 47' W, 110 m, 16 I 1988, *Aymard* 6522 (VEN 268986); mun. Atures, 75 km S de Puerto Ayacucho, 05° 05' N, 67° 40' W, 120 m, 06 IV 2005, *Aymard* 12599 (VEN 394282, PORT s.n.); río Negro, at base of cerro Cucuy, 02 III 1944, *Baldwin* 3204 (VEN 486); depto. Casiquiare, alrededores de Yavita (río Temi) y cerca de la carretera Yavita-Pimichín hacia el km 5 hacia Pimichín, 125–140 m, 6–19 VII 1969, *Bunting* 3845 (MY 21013, U bc 283470, VEN 295452); depto. Atabapo, en los alrededores de Canaripó, en la margen izquierda (S) del bajo río Ventuari, ca. 20 km al E de la confluencia con el río Orinoco, 04° 03' N, 66° 49' W, 98 m, 01 VI 1978, *Huber* 1993 (NY s.n., VEN 213719); río Ventuari, from mouth of río Parú to Las Carmelitas, 19 II 1950, *Maguire* 31572 (NY s.n.); río Pasimoni, 01° 28' 40,7" N, 66° 33' 12,5" W, 28 I 2005, *Redden* 3386 (PORT 94438, VEN 386123); Canaripó, lado S del río Ventuari, 04° 05' N, 66° 50' W, 28 XII 1976, *Steyermark* 112820 (U bc 283484, VEN 117884); alto Orinoco, selvas de Yavita, 128 m, 02 II 1942, *Williams* 14133 (G bc 374713, VEN 11241); caño Pavón, río o caño San Miguel, río Guainía, alto río Negro, 125–127 m, 26 III 1942, *Williams* 14902 (G bc 374601, G bc 374601, MY 58493, NY s.n., VEN 284817); alto río Negro, Guainía, Pimichín, 127 m, 01 IV 1942, *Williams* 14943 (VEN 284816); alto Casiquiare, Capihuara, 120 m, 26 V 1942, *Williams* 15565 (VEN 284818).

A new color form of *Helianthus angustifolius* L.**John Michael Kelley**

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ABSTRACT

A uniquely colored form of *Helianthus angustifolius* was discovered by Rob McElwee of Coushatta, Louisiana and is described here. *Helianthus angustifolius* f. *bicolor* has ligules which are reddened at their base and darker red stems than typical. Published online www.phytologia.org Phytologia 104(3): 40-44. (September 20, 2022). ISSN 030319430.

KEY WORDS: Forma, Louisiana, anthocyanin

Helianthus angustifolius L. is a short-lived perennial sunflower, from fibrous roots, with golden-yellow rays and reddish-brown disks, which inhabits moist grassland habitats throughout the southeastern United States (Correll and Johnson 1970, Steyermark 1963, Weakley 2022).



Lifelong plant enthusiast Rob McElwee, of Coushatta, Louisiana, stumbled across a very distinct color-form of *Helianthus angustifolius* in the Fall of 2020 (Fig. 1). The ligules were distinctly reddened toward their bases (see Fig. 2). The plants re-emerged and bloomed in 2021, which afforded me a closer examination.

Figure 1. Rob and his sunflowers at the type locality.

After hearing of Rob's discovery, I examined numerous herbarium sheets of *Helianthus angustifolius* digitized online (SERNEC 2020), but found none with similar pigmentation patterns. I then consulted experienced researchers of the Southeastern flora and spoke with horticulturists in Louisiana who had seen similar plants. The researchers had not encountered this type of coloration in *Helianthus angustifolius* or any other perennial members of *Helianthus*. Similar forms of *Helianthus annuus* are under cultivation, but these resulted from hybridization (Byrne and Marek 2020). One researcher postulates that the mechanism at play in the ligule coloration might be a mutated replacement of anthocyanins in the place of flavonoids. Rick Johnson, longtime curator of Briarwood Nature Preserve in Natchitoches parish, reported that bicolored plants had grown for years in a wildflower meadow onsite, and upon visiting I found a single representative plant. Buddy Lee, a Nurseryman of Tangipahoa parish, reported seeing similar plants in his region around 2009. Nurseryman Rick Webb reported that he successfully grew plants with this ligule coloration for a few years, but they eventually died. These reports suggest that the form is recurring in Louisiana, but no geographic range is yet clear. Though Rob is attempting to grow the plant from seed and clump division, each horticulturist I spoke with remarked on the difficulty of growing this species beyond one or two seasons. Steyermark (1963) also mentioned this difficulty.

Very few subspecific taxa of *Helianthus angustifolius* have been named, and the few previously published were defined by leaf characters (Fernald 1947; Mohr 1901). Based on evidence that this coloration is novel in perennial sunflowers and occurs sporadically in multiple populations, I propose the following name for Rob's discovery:

***Helianthus angustifolius* forma *bicolor* J.M. Kelley f. nov. - TYPE: USA. Louisiana.** Natchitoches Par.: on Rob McElwee's property along a woodline, [25-35] plants scattered in a colony 20'x10', soil mapped as Shatta series, Parish road 110, coord. 31.983608, -93.223673, 2021, J.M. Kelley 784 with R. McElwee (holotype: LSU). (Figs. 2-4).

DIAGNOSIS

Similar to the typical form, except with ligules reddened proximally, somewhat like *Coreopsis tinctoria*, and with stems noticeably more reddened. This form is apparently recurring in Louisiana populations. It should be sought and annotated to clarify its range. The coloration suggests interesting chemical or genetic variance not yet investigated in the species.

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Figure 2. Range in color on plants of forma bicolor. Most plants with reddened ligules have a consistent amount of color on all heads with some plants being very dark and others lighter.



Figure 3. Stem color of typical form (left) and forma bicolor (right).



Figure 4. Type specimen after fully drying.

***Quercus prinoides* (Fagaceae): a new oak for the Texas flora**

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ABSTRACT

On 1 July 2021, a population of dwarf chinkapin oak (*Quercus prinoides*) was discovered in a small drainage on the east slopes above Sanders Creek, below the dam at Pat Mayse Reservoir, in Lamar County, Texas. Many recent publications have excluded the species from Texas. However, early botanical literature has included the species as occurring in Texas. Its occurrence in northeast Texas is not unexpected given the widespread distribution of the species in eastern Oklahoma, particularly neighboring Choctaw County (just across the Red River). Additional populations should be sought along sandy wooded drainages near the Red River in northeast Texas to accurately determine its actual conservation status in the state. *Published online www.phytologia.org Phytologia 104(3): 45-48 (September 20, 2022). ISSN 030319430.*

KEY WORDS: Fagaceae, dwarf chinkapin oak, Texas, Lamar County, *Quercus*.

Quercus prinoides Willd., dwarf chinkapin oak, or sometimes dwarf chestnut oak is a shrublike to small sized tree in the white oak group (subgenus *Leucobalanus*). The scalloped leaf margins bear a superficial resemblance to chinkapin oak (*Q. muehlenbergii* Engelm.). Some botanists have considered the two to be conspecific, but this view has not prevailed in recent years and most now treat the two species as distinct (Stein et al. 2003).

The species is listed as present in Texas by Coulter (1891), Small (1903), and Vines (1977) all without reference to specimens or locations. Others such as Stein et al. (2003), Kartesz (2015), and USDA, NRCS (2021) excluded the species from the state.

Twenty-four *Quercus prinoides* plants, ranging from presumably mature trees that were estimated 3-4.5 m tall and 12-15 cm DBH, to very small shrubby trees 1-1.5 m tall and less than 2.5 cm diameter were found at the location below (Figs. 1 and 2). The stature of the trees agrees with Sargent (1895) who reported: "In the prairie regions of Missouri and Kansas [the plants are] almost tree-like in habit." Leaf blades possessed mostly 5-7 secondary veins typical of *Q. prinoides*, which is described as possessing 5-8(-9) secondary veins as opposed to *Q. muehlenbergii* that typically possesses 10 or more secondary veins on each side of leaf blade (Nixon 1997; Fig. 3).



Figure 1. *Quercus prinoides* habitat near Pat Mayse Reservoir in Lamar County, Texas.

Voucher specimen. Texas. Lamar Co.: Near Pat Mayse Reservoir Dam 0.3 mi N of Hwy 906, 1 July 2021, *Singhurst and White 22410* (BAYLU).

Dwarf chinkapin oak, has a wide distribution in eastern North America. The map produced by the Biota of North America (Kartez 2015) shows the species to have two centers of distribution plus a scattering of additional records. One center is west of the Mississippi River, in the Interior Highlands of central and southeastern Oklahoma north through eastern Kansas and (rarely) into extreme eastern Nebraska, western Missouri, southern Iowa and northcentral Arkansas. Outlier populations are in the Panhandle of Oklahoma as well as in central Louisiana. East of the Mississippi River the species is most common in the Northeast and Upper Midwest—from Massachusetts, southern New Hampshire, and Vermont, locally in New York and more widespread in New Jersey and Pennsylvania. It is listed as extirpated in Ohio, scattered south of Pennsylvania and generally uncommon to rare south through Appalachia to Alabama and Mississippi.

Habitats vary throughout its range, but include pine barrens, scrublands, forest margins, prairies, and exposed ridges, on deep sands or dry shale, and is rarely reported on calcareous soils (Nixon 1997). The species occurs on the edge of the Great Plains where it is reported to inhabit “dry exposed soils in woods, on bluffs, and along roadsides and forest margins” (Kaul 1986). Stein et al. (2003) describe the habitat as dry sandstone or shale outcrops.

The Lamar County *Quercus prinoides* site occurs on Woodtell loam soils on 5-12% slopes, which are deep loamy and shaly upland soils (Ressell 1979; Fig. 1 and 2). The habitat is oak and hickory forest with scattered pine.



Figure 2. *Quercus prinoides* foliage near Pat Mayse Reservoir in Lamar County, Texas.



Figure 3. *Quercus prinoides* subsurface leaf blade near Pat Mayse Reservoir in Lamar County, Texas.

Associated trees include *Pinus echinata*, *Quercus velutina*, *Q. stellata*, *Carya alba*, *Fraxinus americana*, *Juniperus virginiana*, *Viburnum rufidulum*, *Vaccinium arboreum*, *Cornus florida*, and *Cercis canadensis*. Shrub and vine layer is composed mostly of *Rhus aromatica*, *Vitis aestivalis*, *Smilax bona-nox*, *S. glauca*, and *Toxicodendron radicans*. Understory herbaceous flora includes *Antennaria parlinii*, *Aristolochia serpentaria*, *Desmodium* spp., *Dichanthelium* spp., *Dioscorea villosa*, *Galium circaeans*, *Monarda russeliana*, *Ruellia caroliniensis*, *Solidago petiolaris*, and *Verbesina helianthoides*. This population was growing in close proximity to small openings populated with prairie vegetation such as *Ceanothus herbacea*, *Eryngium yuccifolium*, *Dalea purpurea*, *Hieracium longipilum*, *Liatris aspera*, *Salvia azurea*, and *Schizachyrium scoparium*.

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Quantifying the vegetative community of a bottomland-floodplain forest within Colorado Bend State Park along the Colorado River

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ABSTRACT

We quantified and analyzed the vegetative composition of a bottomland-floodplain forest along the Texas Colorado River within Colorado Bend State Park. This forest contained three vegetational layers: an upper canopy of larger trees including pecan (*Carya illinoiensis*), green ash (*Fraxinus pennsylvanica*), and cedar elm (*Ulmus crassifolia*); a thick under canopy of shrubby species such as gum bumelia (*Sideroxylon lanuginosum*), with mustang grape (*Vitis mustangensis*) and saw greenbrier (*Smilax bona-nox*) as common lianas; and an herbaceous zone of mostly broadleaf woodoats (*Chasmanthium latifolium*) and Canada wild rye (*Elymus canadensis*). Additionally, native invasive plant species were heavily present in both upper and under canopy areas of the sample area. Of six quadrats where diameter at breast height was recorded for 1,162 trees total, 790 were *Juniperus* trees or shrubs. Woody species in the upper and under canopy areas showed little regeneration, possibly due to dense shade contributed by shrubby species and to populations of whitetail deer (*Odocoileus virginianus*) and feral hog (*Sus scrofa*) in the park. We compared the data collected at Colorado Bend State Park, land that has not been grazed by livestock at least since the land was purchased by the state in 1984, to those of another site along the river which has been continuously grazed for at least 100 years, allowing us to evaluate effects that grazing by livestock has on riparian vegetation. Furthermore, the vegetative composition from this western portion of the Texas-Colorado River can be compared to other bottomland and floodplain forests along rivers in the eastern Cross Timbers and Prairie ecoregion of Texas. *Published online www.phytologia.org Phytologia 104(4): 49-65 (December 21, 2022).*
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Freshwater ecosystems make up 0.8% of the earth's surface (Cardinale et al. 2020), with 0.58% of earth's surface being rivers and streams (Allen and Pavelsky 2018). Freshwater habitats support a tenth of animal species but are also being degraded by anthropogenic activities (Strayer and Dudgeon 2010). Riparian areas are the ecotonal junctions between rivers and adjacent terrestrial ecosystems (Gregory et al. 1991). They offer valuable resources for humans and other organisms, provide habitats that promote biodiversity (Strayer and Dudgeon 2010), act as corridors for wildlife (Davis and Hardy 2015), and contain adapted vegetation which creates natural buffers between land types (Richardson et al. 2007). Bottomland-floodplain forests are part of deciduous forests that extend into the floodplain of the riparian zone (Vankat 1943). In 1999, it was estimated that more than 60% of the bottomland and floodplain ecosystems that existed in Texas were lost, and that remaining intact forests are endangered (Barry and Kroll 1999).

Globally, river systems have been divided and associated riparian habitat fragmented by more than one million dams (Jackson et al. 2001) with resulting changes in the hydrologic regime and vegetation communities. River bodies have been reshaped by dredging and modified with levees and dams to allow

easier navigation for water vehicles and aid in flood control (Jackson et al. 2001; Strayer and Dudgeon 2010). Water slowed by or trapped in a reservoir will lose and not reaccumulate as many sediments and minerals as a free-flowing river with a natural deposition and erosion cycle (Strayer and Dudgeon 2010; Duke 2015). Timing of manual flood releases from dams can also cause issues with riparian ecological processes by disrupting seed dispersal or survival of newly rooted plants (Duke 2015). If the anthropogenic flood regime dominates the ecological timing of floods, terrestrial environments adjacent to rivers may be at risk of degradation.

For centuries, humankind has settled along rivers to utilize fresh sources of running water and nutrient-rich lands as convenient sites for homes, farms, and industries (Strayer and Dudgeon 2010). Settlement along riverbanks results in clearing of forested areas to make room on nutrient-rich riparian land for crops and livestock. Forage crops are often planted in these cleared-forest areas and expand into riparian zones. Nonnative grasses expanding into bottomlands can be problematic as they commonly outcompete native tall grasses that are essential to soil integrity and riverbank stability (Jones-Lewey 2016). Forage crops generally serve the purpose of feeding domestic livestock, the presence and abundance of which often destroys vegetation through overgrazing and creates conditions for runoff and erosion (Texas Parks and Wildlife Department (TPWD) 2017). Manure can introduce bacteria and viruses; rising bacterial levels can degrade water quality while viruses can jeopardize organisms in these environments (TPWD 2017). If fields are treated with fertilizer or pesticides, there is potential for these to leech into the water system through soil, or surface water runoff (TPWD 2017). In the United States, 60-70% of pesticide use is administered by the agricultural sector (TPWD 2017), and aquatic ecosystems in the vicinity are especially susceptible to adverse effects from pesticides. Riparian zones can aid in reducing runoff from entering the river system (Nelle 2015), but only if there is adequate vegetation to create the buffer.

Once humans stop use of a riparian zone it is often left to recover without management. When this happens, invasive species become dominant, and services provided by the natural riparian zone are altered. Common invasive grasses intended for turf or yard cover can serve the same groundcover function in the floodplain understory once established, but do not provide the extent of erosion-protection and bank stability that native tall grasses do during floods (Jones-Lewey 2016). Rangeland brush invasion of Ashe's juniper (*Juniperus ashei*) and Pinchot's juniper (*Juniperus pinchotii*) has been documented for decades in the Cross Timbers ecoregion of Texas, and their encroachment into bottomland forests has caused riparian land to become drier, potentially impeding health of larger hardwood tree species native to these areas (Vickery 1991). As a result of invasive species encroachment, biodiversity of riparian ecosystems is reduced (TPWD 2017).

Due to the many factors working against healthy, natural riparian ecosystems, managed restoration is needed. Before restoration efforts can be made in a riparian area, the vegetative community needs to be quantified and described, so restoration efforts are based on the measured state relative to reference ecosystems that reflect natural vegetative communities within different ecosystems of Texas (Cotton 2017). There are many rivers in Texas, yet proper quantification of forest communities is lacking for a considerable amount of Texas (Diamond et al. 1987). The more information we have on vegetative communities in riparian areas, the better we can compare and potentially develop ubiquitous strategies for preserving and restoring riparian forests.

The Texas Colorado (TXCO) River is the fifth longest river in the state. Yet, the first vegetative analysis of a portion of its riparian zone was not published until 2018, when the woody and herbaceous composition at the Timberlake Biological Field Station (TBFS) was defined (Nelson et al. 2018). The study site at TBFS was a bottomland forest located in the Lampasas Cut Plain along the TXCO River. The forest consisted of three vegetational layers: 1) upper canopy with cedar elm (*Ulmus crassifolia*) and green ash (*Fraxinus pennsylvanica*) as dominant trees, 2) under canopy of heavily browsed lianas, shrubs and smaller trees including saw greenbrier (*Smilax bona-nox*), Texas persimmon (*Diospyros texana*), and western

soapberry (*Sapindus saponaria*), 3) herbaceous zone of Canada wild rye (*Elymus canadensis*) and Texas wintergrass (*Nasella leuchothricha*), with sedges and forbs (Nelson et al. 2018). The sampling area was grazed by livestock for ≥ 100 years, frequented by a resident herd of white-tailed deer (*Odocoileus virginianus*), and showed evidence of American beaver (*Castor canadensis*) browsing and girdling trees (Nelson et al. 2018). This herbivory and the hydrological changes to the river could be the causes of the sparse regeneration of the dominant trees, cedar elm and green ash (Nelson et al. 2018).

Colorado Bend State Park (CBSP) was purchased by Texas in 1984 and is located on the TXCO River about 30 km downstream of TBFS (TPWD-History). Domestic livestock have not been present at CBSP since its acquisition by the state. Like many other riparian forests in Texas, little has been done to quantify vegetative communities at CBSP. During part of a field survey to determine diversity of the rodent community within CBSP, six tree species and some herbaceous understory categories, and their percent coverage as habitat were recorded in two transects set in riparian forest (Scales and Wilkins 2003). However, the species of the herbaceous zone were not identified. Ecological site descriptions of forests need more detail and must include canopies and understory (Nelson et al. 2018).

The objectives of the investigation were to quantify both woody and herbaceous species of riparian areas within CBSP and provide ecotonal information regarding the Edwards Plateau and Cross Timbers ecoregions. Additionally, vegetative community composition from CBSP was compared to that of TBFS to evaluate CBSP as a potential reference site for restoration.

MATERIALS AND METHODS

FIELD METHODS

Sampling took place in riparian areas along the TXCO River at CBSP on October 11-13 and 18-20 of 2019. Surveyor measuring tapes were used to set up 12 nonpermanent quadrats (sampling plots) within a stretch of the forest along the west bank of the river. The quadrats measured 50 m by 25 m with the longest side running parallel to the river. Whenever there was not enough bottomland between the river and upland, quadrats consisted of two 50 m by 12.5 m combined sample areas. Sampling began at the River Trail head near the park headquarters and quadrats were set up every 0.2 km. GPS coordinates for the four corners of each quadrat were recorded.

All quadrats were sampled for woody vegetation, any individual with a diameter at breast height (DBH) measurement of ≥ 1 cm was recorded. To provide the description of the vegetative community, the woody and herbaceous vegetation data from the first six quadrats located closest to the River Trail head were compiled. Herbaceous vegetation was sampled using the step-point method (Bonham 1989) to quantify the species that form the understory. For this method a metal rod is used to strike the ground as the surveyor walks. If the rod strikes a plant, then the plant is identified and recorded; each strike with no plant is recorded as bare ground. The surveyor does not look at the ground until after the rod lands to reduce surveyor bias. A minimum of 500 points were taken at each quadrat for a total of 3,185 total points recorded in the six quadrats.

Woody and herbaceous species were identified and listed with common and scientific names using the taxonomic keys in Diggs et al. (1999), and most were identified to species level. Any unidentifiable plants were labelled as an unknown accompanied by an accurate taxonomic describer. Voucher specimens were collected and deposited in the herbarium at Tarleton State University (TAC).

STATISTICAL ANALYSIS

DBH measurement totals per species were used to calculate area (m^2), which allowed for calculating dominance (m^2/ha). Densities (plants/ha), frequencies, coverages, and relative importance values were

found, as demonstrated by Ford and Van Auken (1982), Wood and Wood (1988, 1989), Rosiere et al. (2013), and Nelson et al. (2018). Richness was determined by counting the species present, and Shannon diversity and evenness were calculated using the ‘vegan’ community ecology package in R Studio (Oksanen et al. 2020).

RESULTS

Three vegetational layers made up the bottomland-floodplain forest: 1) upper canopy of larger trees including pecan (*Carya illinoiensis*), green ash (*Fraxinus pennsylvanica*), and cedar elm (*Ulmus crassifolia*), 2) under canopy thick with short trees and shrubs including *Juniperus* trees and gum bumelia (*Sideroxylon lanuginosum*), with mustang grape (*Vitis mustangensis*) and saw greenbrier (*Smilax bona-nox*) as common lianas, 3) herbaceous zone where main vegetation consisted of native grasses like broadleaf woodoats (*Chasmanthium latifolium*) and Canada wild rye (*Elymus canadensis*), however much of this zone was relatively barren (Tables 1 and 2).

Table 1. Density, dominance, and relative importance values for woody vegetation greater than or equal to one centimeter diameter at breast height of the bottomland-floodplain forest in Colorado Bend State Park, along the Texas-Colorado River.

Common name (Scientific name)	Density (plants/ha)	Dominance (m ² /ha)	Importance Value (%)
American elm (<i>Ulmus americana</i>)	8.0	4.0	1.6
Black walnut (<i>Juglans nigra</i>)	1.3	0.1	0.5
Cedar elm (<i>Ulmus crassifolia</i>)	104.0	33.7	5.0
Chinaberry (<i>Melia azedarach</i>)	1.3	<0.1	0.5
Green ash (<i>Fraxinus pennsylvanica</i>)	38.7	93.8	4.8
Gum bumelia (<i>Sideroxylon lanuginosum</i>)	65.3	3.0	4.2
<i>Juniperus</i> spp.	1053.3	2303.1	54.6
Mexican plum (<i>Prunus mexicana</i>)	1.3	0.1	0.5
Mustang grape (<i>Vitis mustangensis</i>)	44.0	1.4	3.7
Pecan (<i>Carya illinoiensis</i>)	28.0	152.7	5.3
Poison ivy (<i>Toxicodendron radicans</i>)	1.3	<0.1	0.5
Prairie flame leaf sumac (<i>Rhus lanceolata</i>)	2.7	<0.1	1.0
Red mulberry (<i>Morus rubra</i>)	2.7	0.1	1.0
Red oak (<i>Quercus buckleyi</i>)	1.3	0.7	0.5
Roughleaf dogwood (<i>Cornus drummondii</i>)	84.0	2.4	3.7
Rusty blackhaw (<i>Viburnum rufidulum</i>)	8.0	<0.1	0.6
Sugarberry (<i>Celtis laevigata</i>)	10.7	0.1	2.1
Sycamore (<i>Platanus occidentalis</i>)	16.0	31.6	2.6
Texas mountain laurel (<i>Dermatophyllum secundiflorum</i>)	2.7	<0.1	0.5
Texas persimmon (<i>Diospyros texana</i>)	62.7	1.3	3.7
Western soapberry (<i>Sapindus saponaria</i>)	8.0	0.1	1.6
Virginia creeper (<i>Parthenocissus quinquefolia</i>)	4.0	<0.1	1.5
Total	1549.3	2628.3	100.0

There were 22 woody species with diameter measurements of ≥ 1.0 cm sampled in this forest. Of these, 18 were native trees, three were native woody vines and lianas, and one was a non-native invasive tree. Among the native trees, *Juniperus* trees were native invasive species encroaching into the bottomlands. *Juniperus* trees were the most common tree with the highest dominance (2303.1 m²/ha) and relative importance value (54.6%) of all woody species measured that were ≥ 1.0 cm in diameter (Table 1). After *Juniperus* trees, cedar elm and roughleaf dogwood (*Cornus drummondii*) were the most common trees. Pecan and green ash had the next highest dominances (152.7 m²/ha and 93.8 m²/ha, respectively) and pecan

and cedar elm had the next highest relative importance values (5.3% and 5.0%, respectively; Table 1). Mustang grape was a common vine which had a fairly high relative importance value (3.7%), the same importance value as two shrubby species, roughleaf dogwood and Texas persimmon (*Diospyros texana*; Table 1). A single non-native invasive chinaberry (*Melia azedarach*) was recorded in the sample area; however, more were observed along the river outside of the sampling area.

Table 2. Step-point counts to determine species composition of herbaceous and woody vegetation that were less than one centimeter diameter at breast height of the bottomland-floodplain forest in Colorado Bend State Park, along the Texas-Colorado River.

Common name (Scientific name)	# of hits (%)
<i>Pteridophytes</i>	
Horsetail (<i>Equisetum hyemale</i>)	181 (5.7)
Total Pteridophytes	181 (5.7)
<i>Grasses</i>	
Bermudagrass (<i>Cynodon dactylon</i>)	4 (0.1)
Broadleaf woodoats (<i>Chasmanthium latifolium</i>)	511 (16.0)
Canada wild rye (<i>Elymus canadensis</i>)	115 (3.6)
Hairy wood brome (<i>Bromus pubescens</i>)	16 (0.5)
Johnsongrass (<i>Sorghum halepense</i>)	21 (0.7)
Little bluestem (<i>Schizachyrium scoparium</i>)	1 (<0.1)
Switchgrass (<i>Panicum virgatum</i>)	5 (0.2)
Unknown grass	43 (1.4)
Total grasses	716 (22.5)
<i>Grasslike</i>	
Unknown sedge	39 (1.2)
Total grasslike	39 (1.2)
<i>Forbs</i>	
Castor bean (<i>Ricinus communis</i>)	1 (<0.1)
Eryngo (<i>Eryngium leavenworthii</i>)	1 (<0.1)
Frostweed (<i>Verbesina virginica</i>)	10 (0.3)
"Orange-stem" <i>Euphorbia</i> sp.	1 (<0.1)
<i>Rubus</i> sp.	2 (0.1)
Slim aster (<i>Aster subulatus</i> var. <i>ligulatus</i>)	3 (0.1)
<i>Tragia</i> sp.	5 (0.2)
Unknown/small dicot	7 (0.2)
Unknown mint	1 (<0.1)
Western ragweed (<i>Ambrosia psilostachya</i>)	3 (0.1)
Wild poinsettia (<i>Euphorbia heterophylla</i>)	1 (<0.1)
Total forbs	35 (1.1)
<i>Shrubs, lianas, and small trees</i>	
Agarito (<i>Mahonia trifoliolata</i>)	1 (<0.1)
American elm (<i>Ulmus americana</i>)	4 (0.1)
Bristle greenbrier (<i>Smilax tamnoides</i>)	11 (0.4)
Cedar elm (<i>Ulmus crassifolia</i>)	43 (1.4)
Green ash (<i>Fraxinus pennsylvanica</i>)	1 (<0.1)
Gum bumelia (<i>Sideroxylon lanuginosum</i>)	16 (0.5)
<i>Juniperus</i> spp.	18 (0.6)
Plateau live oak (<i>Quercus fusiformis</i>)	1 (<0.1)
Mustang grape (<i>Vitis mustangensis</i>)	2 (0.1)
Nandina (<i>Nandina domestica</i>)	1 (<0.1)
Poison ivy (<i>Toxicodendron radicans</i>)	1 (<0.1)
Prairie flame leaf sumac (<i>Rhus lanceolata</i>)	2 (0.1)

Table 2 (cont.)

Roughleaf dogwood (<i>Cornus drummondii</i>)	13 (0.4)
Saw greenbrier (<i>Smilax bona-nox</i>)	93 (2.9)
Sugarberry (<i>Celtis laevigata</i>)	1 (<0.1)
Texas mountain laurel (<i>Dermatophyllum secundiflorum</i>)	1 (<0.1)
Texas persimmon (<i>Diospyros texana</i>)	7 (0.2)
Virginia creeper (<i>Parthenocissus quinquefolia</i>)	5 (0.2)
Western soapberry (<i>Sapindus saponaria</i>)	1 (<0.1)
Total shrubs, lianas, and small trees	222 (7.0)
<i>Bare ground</i>	1992 (62.5)
Total hits	3185 (99.8)

Of the 40 species in the understory (<1 cm), 28 were native, one was a native invasive, and four were non-native species; seven plant species were not identifiable to species level. There was a substantial presence of horsetail (*Equisetum hyemale*) which had the second highest percentage of herbaceous vegetation (5.7%; Table 2). Broadleaf wood oats (16.0%) and Canada wild rye (3.6%) are native grasses that were main components of the herbaceous zone, and a total of 22.5% of the understory was comprised of grasses. Non-native invasive grasses included Johnsongrass (*Sorghum halepense*, 0.7%) and Bermudagrass (*Cynodon dactylon*, 0.1%; Table 2). While these low percentages of invasive grasses are encouraging, both Johnsongrass and Bermudagrass are described as species that can outcompete other grasses and become dominant in bottomland systems (Elliott 2014). Sedge species were not identifiable at the time of sampling but were likely native and made up 1.2% of the understory (Table 2). Overall, forbs did not contribute much to the herbaceous zone (1.1%), but frostweed (*Verbesina virginica*) was the most common forb species (0.3%; Table 2). There was one non-native herbaceous shrub, castor bean (*Ricinus communis*, <0.1%), which was sampled a single encounter in the study area (Table 2), however established mature stands of castor bean were seen in multiple areas along the riverbank. Saw greenbrier was fairly common (2.9%) in the understory (Table 2) and was notably climbing and hanging from the upper canopy and shrubby trees in many of the sampling sites, however, individual stems were never thick enough to measure and record DBH in these locations. Cedar elm was the woody species in the understory with the most seedlings (1.4%) and highest sampled regeneration rates (Table 2). *Juniperus* seedlings (0.6%) were the only native invasive woody species sampled. Nandina (*Nandina domestica*, <0.1%) was the only non-native woody shrub and was sampled one time in the study area.

CBSP is located in the Edwards Plateau ecoregion of the TXCO river, and TBFS in the Cross Timbers ecoregion, with CBSP being a possible candidate as a reference site for TBFS. CBSP had shallower soils with bedrock closer to the surface than the sites at TBFS. Vegetation densities, dominances and relative importance values at the sites were directly compared (Table 3). These two TXCO River sites had 15 species in common: 12 were trees, shrubs, or lianas, two were grasses, and one was a forb (Tables 1 and 2; Nelson et al. 2018). At CBSP, *Juniperus* trees yielded the highest density (1053.3 plants/ha), dominance (2303.1 m²/ha) and relative importance value (54.6%; Table 3), while only one *Juniperus* seedling or sapling was sampled by step-point method in the TBFS herbaceous understory (Nelson et al. 2018). Cedar elm was the woody species at TBFS with the highest density (222.7 plants/ha), dominance (1036.8 m²/ha) and relative importance value (70.7%; Table 3; Nelson et al. 2018). At TBFS, cedar elm was about twice as dense, three-hundred times as dominant, and had relative importance about fourteen times greater than in CBSP (Table 3). Cedar elm in CBSP had the second highest density (104.0 plants/ha), and third highest relative importance (5.0%) of the present woody species and was also the tree with the highest regeneration (1.4%) in the herbaceous understory (Table 3). Juniper, pecan, and gum bumelia were important in CBSP, but were not at TBFS (Table 3; Nelson et al. 2018). Alternatively, American elm, sugarberry, and western soapberry had high importance values at TBFS, but not at CBSP (Table 3; Nelson et al. 2018).

CBSP had about twice the amount of bare ground step-points (Table 3; Nelson et al. 2018). Broadleaf woodoats and horsetail were sampled often at CBSP but were not sampled at TBFS (Table 3; Nelson et al. 2018). Texas winter grass (*Nasella leuchothricha*) and Bermudagrass were more frequently sampled at TBFS (Table 3; Nelson et al. 2018). At TBFS, grasses made up twice as much herbaceous vegetation in the understory (44.3%; Nelson et al. 2018) than grasses at CBSP. Canada wild rye was almost half (20.6%) of the total grass composition, which is more than five times the amount of Canada wild rye in the understory of CBSP (Table 3; Nelson et al. 2018). Saw greenbrier was nearly twice as common in the CBSP herbaceous zone as it was in TBFS (Table 3; Nelson et al. 2018).

Table 3. Comparison of the Colorado Bend State Park bottomland-floodplain forest to the bottomland forest at Timberlake Biological Field Station (Nelson et al. 2018). Woody vegetation is sorted by five highest densities (plants/ha), dominances (m^2/ha), and relative importance values (%), and top five herbaceous vegetation based on number of hits (%) are compared between the two locations.

	CBSP	TBFS
<i>Woody Vegetation Data</i>		
Highest density 1 (plants/ha)	Junipers 1053.3	Cedar elm 222.7
Highest density 2	Cedar elm 104.0	Western soapberry 46.7
Highest density 3	Roughleaf dogwood 84.0	Green ash 45.3
Highest density 4	Gum bumelia 65.3	Sugarberry 25.3
Highest density 5	Texas persimmon 62.7	American elm 24.0
Highest dominance 1 (m^2/ha)	Junipers 2303.1	Cedar elm 1036.8
Highest dominance 2	Pecan 152.7	Green ash 204.9
Highest dominance 3	Green ash 93.8	American elm 37.1
Highest dominance 4	Cedar elm 33.7	Prickly-pear cactus 16.8
Highest dominance 5	Sycamore 31.6	Sugarberry 14.9
Highest importance value 1 (%)	Junipers 54.6	Cedar elm 70.7
Highest importance value 2	Pecan 5.3	Green ash 14.1
Highest importance value 3	Cedar elm 5.0	Western soapberry 4.5
Highest importance value 4	Green ash 4.8	American elm 3.9
Highest importance value 5	Gum bumelia 4.2	Sugarberry 2.9
<i>Herbaceous Vegetation Data</i>		
Highest number hits 1 (%)	Broadleaf woodoats 16.0	Canada wild rye 20.6
Highest number hits 2	Horsetail 5.7	Texas wintergrass 15.2
Highest number hits 3	Canada wild rye 3.6	Bermudagrass 5.0
Highest number hits 4	Saw greenbrier 2.9	Gotthilf Muhlenenberg's caric-sedge 3.4
Highest number hits 5	Cedar elm 1.4	Unknown caric sedge 2.5
	Unknown grass 1.4	Southwestern bristlegrass 2.4
Bare ground	62.5	35.6

Diversity measures were relatively similar between CBSP and TBFS, except for woody richness, which was highest at CBSP with 22 species, compared to 13 species in TBFS (Table 4; Nelson et al. 2018). Herbaceous richness of the forest along the TXCO River was equal at 40 species (Table 4; Nelson et al. 2018). Woody and herbaceous evenness and Shannon Diversity were slightly lower for CBSP than for TBFS (Table 4).

Table 4. Richness, Evenness, and Shannon Diversity comparisons of Colorado Bend State Park bottomland-floodplain forest to the Timberlake Biological Field Station bottomland forest (Nelson et al. 2018).

	TXCO River (CBSP)	TXCO River (TBFS)
Woody Richness > 1.0 cm	22	13
Herbaceous Richness < 1.0 cm	40	40
Woody Evenness > 1.0 cm	0.44	0.59
Herbaceous Evenness < 1.0 cm	0.57	0.66
Woody Shannon Diversity > 1.0 cm	1.37	1.51
Herbaceous Shannon Diversity < 1.0 cm	2.12	2.42

Due to *Juniperus* species' invasive habit, juniper data were removed from Table 1 to show shifted relative importance values of other woody species (Table 5). With junipers removed, Pecan became the species with the highest relative importance value (20.6%), followed by green ash (15.3%), cedar elm (13.0%), roughleaf dogwood (7.9%), and gum bumelia (7.7%; Table 5). Green ash became more important than cedar elm, and roughleaf dogwood became more important than gum bumelia, when juniper data was excluded from woody vegetation calculations (Table 5).

Table 5. Density, dominance, and relative importance values for woody vegetation greater than or equal to one centimeter diameter at breast height of the bottomland-floodplain forest in Colorado Bend State Park, along the Texas-Colorado River when *Juniperus* species data are excluded.

Common name (Scientific name)	Density (plants/ha)	Dominance (m ² /ha)	Importance Value (%)
American elm (<i>Ulmus americana</i>)	8.0	4.0	2.4
Black walnut (<i>Juglans nigra</i>)	1.3	0.1	0.6
Cedar elm (<i>Ulmus crassifolia</i>)	104.0	33.7	13.0
Chinaberry (<i>Melia azedarach</i>)	1.3	<0.1	0.6
Green ash (<i>Fraxinus pennsylvanica</i>)	38.7	93.8	15.3
Gum bumelia (<i>Sideroxylon lanuginosum</i>)	65.3	3.0	7.7
Mexican plum (<i>Prunus mexicana</i>)	1.3	0.1	0.6
Mustang grape (<i>Vitis mustangensis</i>)	44.0	1.4	6.1
Pecan (<i>Carya illinoensis</i>)	28.0	152.7	20.6
Poison ivy (<i>Toxicodendron radicans</i>)	1.3	<0.1	0.6
Prairie flame leaf sumac (<i>Rhus lanceolata</i>)	2.7	<0.1	1.2
Red mulberry (<i>Morus rubra</i>)	2.7	0.1	1.2
Red oak (<i>Quercus buckleyi</i>)	1.3	0.7	0.7
Roughleaf dogwood (<i>Cornus drummondii</i>)	84.0	2.4	7.9
Rusty blackhaw (<i>Viburnum rufidulum</i>)	8.0	<0.1	1.0
Sugarberry (<i>Celtis laevigata</i>)	10.7	0.1	2.8
Sycamore (<i>Platanus occidentalis</i>)	16.0	31.6	6.3
Texas mountain laurel (<i>Dermatophyllum secundiflorum</i>)	2.7	<0.1	0.7
Texas persimmon (<i>Diospyros texana</i>)	62.7	1.3	6.9
Western soapberry (<i>Sapindus saponaria</i>)	8.0	0.1	2.0
Virginia creeper (<i>Parthenocissus quinquefolia</i>)	4.0	<0.1	1.8
<i>Total</i>	496.0	325.3	100.0

DISCUSSION

Woody Vegetation

The most recent known study that occurred within the park, which provided some information on six woody species, was a rodent survey with two riparian trapping transects (Scales and Wilkins 2003). Specific information about each species is lacking and all are grouped together as “woody plants” which made up the main vegetative cover component (46%) of the habitat being assessed (Scales and Wilkins 2003). Of the trees noted in the rodent survey, black walnut (*Juglans nigra*), red oak (*Quercus buckleyi*), and plateau live oak (*Quercus fusiformis*) were only sampled one time each within the current study’s sample area, making them rare in the current riparian forest. Both the red oak and the black walnut appeared to be mature individuals. One plateau live oak seedling was sampled in the step-point surveys, but adult trees were only observed more in upland areas adjacent to the riparian forest. This could indicate a loss of regeneration and reduction in abundance of these species within the last 20 years.

The amount of juniper sampled in CBSP appears to greatly exceed that of other various riparian forests in Texas with documented *Juniperus* presence. In the current study, Ashe’s juniper (*Juniperus ashei*) and eastern red cedar (*Juniperus virginiana*) were the two species of juniper identified. Both species are documented by Texas Ecosystem Analytical Mapper (TEAM), however Ashe’s Juniper seems to be the more common species of juniper in the Hill Country. Ashe’s juniper was a dominant species with an importance value of 20.9 ± 12.7 in creek bottoms in the Cedar Brakes region of the southern Edwards Plateau (Van Auken et al. 1979). In a phytosociological study of riparian forests along the Guadalupe River, Ashe’s juniper was limited to the upper portion of the floodplain (Ford and Van Auken 1982); and in a follow-up investigation of flood-caused changes to vegetation along the upper Guadalupe River, Ashe’s juniper was present in the riparian forest, but reported as a low-density species (Van Auken and Ford 2017). Along the Sabinal River, Ashe’s juniper was a high-density species with a relative importance value of 2.98% (Wood and Wood 1989) and on the Frio River, its relative importance was 2.75% (Wood and Wood 1988). Hall (1952) was perhaps the first account of both species existing and potentially hybridizing in the Edwards Plateau. Eastern red cedar is either not specified or nonexistent in much of the previous riparian work conducted in the Edwards Plateau. Both species have invaded much of the Great Plains of the United States, and are particularly problematic in tallgrass prairie, bottomlands hardwood forest and upland post oak-forest ecosystems in the Cross Timbers (Bidwell et al. 2016).

Pecan, despite lower density, contributed greatly to dominance and garnered a high importance value at CBSP because they were generally larger trees and because their size could be characterized as old growth. Similarly, in a study conducted in the West Cross Timbers ecoregion, pecan was not highly dense, but was the second most dominant tree and of second high relative importance to the bottomland forest along the Bosque River (Rosiere et al. 2013). Results from a study over flooding that caused changes along the Guadalupe River revealed that pecan average basal area decreased post-flood (Van Auken and Ford 2017), which could indicate that while pecans exist and persist in riparian settings, they are moderately intolerant to the regular flooding expected in riparian areas.

Green ash is described as one of three riparian indicator species in Texas and is specifically indicative of regular disturbance attributed to frequent flooding in an area (Duke 2015). Many green ashes at CBSP were close to the river’s edge, which corresponds with the species’ root system adaptations that allow green ash trees to dominate stream sides and steep riverbank slopes where many species cannot survive (Duke 2015). These extensive root systems also benefit the slopes, which are most prone to direct erosion by the river. Low regeneration rate of green ash was likely due to the fruits and foliage of green ash being highly palatable for many wildlife species (Duke 2015). Herbivory by white-tailed deer, cattle, and beaver, was the apparent cause of low green ash regeneration rates at TBFS as well (Nelson et al. 2018).

One young Chinaberry (*Melia azedarach*) was the only non-native tree >1.0 cm. sampled in CBSP. Chinaberry was introduced from Asia (Jones-Lewey 2016) and listed as a common exotic plant with invasive attributes (Nelle 2015), as it tends to crowd out native species in riparian areas. There is documentation of Chinaberry occurring in many riparian forests across Texas (current study; Nelson et al. 2018; Van Auken and Ford 2017; Rosiere et al. 2013; Davis and Smith 2013; Longfield 2001; Nixon et al. 1991; Wood and Wood 1989; Wood and Wood 1988; Van Auken and Bush 1985; Bush and Van Auken 1984; Ford and Van Auken 1982). Chinaberry may not be as common along the TXCO River in CBSP due to infrequent flooding, as Chinaberry tends to establish after flooding (Bush and Van Auken 1984) and perhaps, because there are few seed sources compared to some rivers.

Some forests in the Cross Timbers contained fewer woody species than the forest at CBSP, only 13 woody species were recorded along the TXCO River at TBFS (Nelson et al. 2018), and 17 woody species were recorded along the Bosque River (Rosiere et al. 2013). Riparian forests from other portions of the Edwards Plateau and Rio Grande Plains yielded higher woody species richness, with 37 on the Leona River and 56 on the Sabinal River (Wood and Wood 1989), 66 along the Frio River (Wood and Wood 1988), and 32 woody species along the Guadalupe River (Ford and Van Auken 1982). In 1993, vegetation of 20 bottomland sites in East Texas were analyzed and revealed presence of 72 woody species, with evenness value ranges from 0.65 to 0.79 (Brooks et al. 1993). Despite having reported lower woody richness, both TBFS and the Bosque River studies had higher evenness values for woody vegetation than CBSP (Nelson et al. 2018) due to the high numbers of junipers in CBSP.

Herbaceous Vegetation

Increased bare ground could be caused by excessive shade and coverage of soil by juniper species (Hoff et al. 2018; Young and Bush 2009). Broadleaf woodoats was potentially the most common species in the understory due to its shade tolerance (Jones-Lewey 2016). Broadleaf woodoats grows readily on slopes and riverbanks, holding soil in place where other soil-stabilizer species may not grow as well (Jones-Lewey 2016) thus preventing excess erosion of the banks. Johnsongrass and Bermudagrass have the potential to become problematic in riparian areas as they can outcompete and replace native riparian grasses (Elliott 2014), potentially increasing erosion rates and degrading nutrient-richness of the soil. Bermudagrass was also present in the understory at TBFS, and likely moved down into the bottomland from nearby fields (Nelson et al. 2018).

Castor bean (*Ricinus communis*), a native to east Africa (Invasive Species Specialist Group (ISSG) 2006), is an escaped ornamental that was recorded once in a step-point sampling area and documented twice outside of our sampling area in large stands on the edge of the TXCO River in the state park. The only other known record of castor bean in riparian areas was along a section of the Frio River, located west of San Antonio in the transitional area between the Edwards Plateau and South Texas Plains ecoregions (Wood and Wood 1988). Here it was described with pecan and honey mesquite as an inner bank stand but was not elaborated on further (Wood and Wood 1988). As an invasive species along rivers, castor bean is problematic for several reasons. Mature castor bean plants rapidly grow to an average of 3 to 5 meters in height and outcompete native species through quickly creating substantial shade and reaching reproductive maturity within the first six months after germination (ISSG 2006). Castor bean is not forage, as its foliage is slightly poisonous, and its seeds are the source of the toxin ricin which can cause illness or death if consumed by any organism; two to six seeds can be fatally toxic to humans and large mammals (ISSG 2006).

Nandina (*Nandina domestica*) is noted as a non-native invasive in the Edwards Plateau, along with *Ligustrum* spp., Chinaberry and Chinese tallow (TPWD 2012). Nandina is native to India and has been reported to escape from cultivation into sandy woods (Diggs et al. 1999). It is possible that Nandina escaped from yards and landscaping from a housing addition located across the river from the park and could become more common in the bottomland overtime.

Hydrology

Indicators of riparian health include an active floodplain, energy dissipation during floods, new plant colonization, stabilizing vegetation, age diversity, species diversity, plant vigor, water storage, and establishment of equilibrium between erosion and deposition (Jones-Lewey 2016). Currently, the TXCO at CBSP is most closely affected by two dams, one located 130 km northwest at Lake O.H. Ivie and the other about 30 km to the south at Lake Buchanan. Dams affect floodplain forests by separating and isolating remnant floodplains, which changes biodiversity in riparian areas (Johnson 2002). The primary disturbance and stressors that influence flood plain forests in semi-arid regions have been associated with river flow where flooding resets the successional cycle (Shafron et al. 2002; Hardy et al. 2015) and provides critical inundation for wetland adapted plants (Dawson et al. 2017). During droughts and flood flow events, low flow hydrology alters riparian vegetation (Nelson et al. 2018; Hardy et al. 2015). Damming of the TXCO River has caused changes in flood magnitude which can limit the occurrence of wetland-adapted species and turned river flow into a limiting factor that may promote upland species (Alldredge and Moore 2014), such as species of juniper. The TXCO River at CBSP seldom inundates the floodplain forest due to changes in hydrology caused by damming, but when it does flood, the flood flow is so substantial that energy is often not dissipated by vegetation, and this results in an imbalance of erosion and deposition (Nelson et al. 2018). Based on the evaluation system of Jones-Lewey (2016) and riparian health indicators, the portion of the TXCO River at CBSP is in at-risk condition and will need management to reduce encroachment by upland species and restore the forest to a highly functional condition.

Herbivory

CBSP has significant populations of white-tailed deer and feral hogs (*Sus scrofa*). During the research, white-tailed deer were observed in the park multiple times, and rooting by feral hogs was also documented. Because state park land is protected and disturbance is minimized by the state, many animal species find sanctuary in the park's boundary, to the point where they become problematic to the environment. Abundance and activities of both white-tailed deer and feral hogs can cause habitat degradation and low regeneration rates of woody species (TPWD 2012) and are likely contributors to low regeneration of woody species, general lack of forbs, and the large percentage of bare ground in the CBSP understory.

White-tailed deer hunting is permitted within the park in specific, assigned areas and only by application and acquisition of a hunting permit by drawing. In past hunting seasons, there have been three different intervals to hunt deer: an antlerless and spike period, a regular period for either sex, and a youth only period for either sex (TPWD-Texas Public Hunt System). These three intervals combined in 2020 consisted of only 18 days. During this short amount of time allotted for hunting in the state park, bag limits were three white-tailed deer per drawn applicant. Additionally, hunters drawn for deer hunts were not limited on the number of feral hogs, aoudad (*Ammotragus lervia*) and other exotic mammals they could take (TPWD-Texas Public Hunt System). There is not information available reporting the numbers of these wildlife species taken per season within the park. The Texas Conservation Action Plan (TCAP) for the Edwards Plateau region states deer in the region are insufficiently harvested, leading to high deer populations and extreme herbivory (The Nature Conservancy 2004), notably on hardwood seedlings (TPWD 2012). Of the woody species recorded in CBSP, cedar elm, poison ivy (*Toxicodendron radicans*), roughleaf dogwood (*Cornus drummondii*), saw greenbrier and Virginia creeper (*Parthenocissus quinquefolia*) are preferred first-choice browse for white-tailed deer (TPWD 2009). Additionally, junipers are among the woody species that are least utilized for browse (TPWD 2009; Wright et al. 2002). White-tailed deer have become a native problematic (TPWD 2012) species in many parts of Texas, especially in the Hill Country which supports the largest population of white-tailed deer in the state (TPWD-Hill Country).

Feral hogs are a non-native invasive (Schlichting et al. 2015) ungulate that are widespread across the state and exhibit foraging behaviors that degrade riparian habitat, which they tend to prefer over upland habitat (Wagner 2004). Two factors contribute to feral hogs quickly becoming problematic: versatile diets and high fecundity. In the Rolling Plains ecoregions of Texas, feral hog diets were analyzed throughout each of the four seasons (Schlichting et al. 2015). Natural vegetation like grasses, forbs, roots, tubers, browse, and mast made up 56.15% of the feral hog annual diet, and agricultural crops essentially made up the remaining portion (42.21%) of the diet (Schlichting et al. 2015). In pristine bottomland forests, where agricultural crops have not been planted in monocultures, established native grasses like broadleaf woodoats and Canada wild rye become valuable forages for grazing and browsing wildlife (Rosiere et al. 2013). Near the Lampasas Cut Plain, soils are deeper and limestone-derived, and CBSP soils within the sampling area are either frequently flooded, deep, loamy Westola, or stony, shallow Eckrant (Web Soil Survey). Rooting and wallowing by feral hogs increase the likelihood of soils eroding more quickly. Feral hog activity along the river also decreases regeneration rates of woody species and causes damage to riverbank stability through increasing erosion rates (Nelle 2015).

Native Juniper Invasion

The floodplain forests of larger rivers, like the TXCO River, should contain truly mesic woody vegetation and mostly exclude upland species (Van Auken et al. 1979), but the forest at CBSP faces encroachment by Ashe's juniper and eastern red cedar. The extent of Ashe's juniper in Texas before European settlers arrived is debated, but the presence of these trees in the Edwards Plateau was described in reports from early explorers (TPWD 2017). Eastern red cedar proliferation and range began to increase into the Cross Timbers in the mid-1900s (Hoff et al. 2018). The juniper invasion in Texas is the result of anthropogenic actions and is directly tied to fire suppression on degraded land (Leis et al. 2017). *Juniperus* species are some of the first to establish in areas degraded by agriculture and where fire is suppressed (TPWD 2017). Prescribed burning currently only occurs on one park trail near an upland savannah (TPWD-Park Trails). It is most likely that fire suppression, lack of brush management, and absence of subsequent management or restorative measures following the park's agricultural history have contributed to the invasion of native junipers.

Ashe's juniper and eastern red cedar can be distinguished by the growth pattern of the trunk where Ashe's juniper characteristically has multiple trunks sprouting from the base, while eastern red cedar typically has one single trunk (Diggs et al. 1999). Another trait that can help differentiate these two species is the shape of the abaxial leaf glands: abaxial glands of Ashe's juniper are round and often conspicuously raised, whereas abaxial glands of eastern red cedar are more elongated or elliptical and not conspicuously raised (Diggs et al. 1999). At CBSP, several individuals of each species were identified using these characters, however multiple individuals exhibited cross-species characteristics. Hybridization and introgression occur when Ashe's juniper and eastern red cedar are both present (Diggs et al. 1999), and hybrid swarms of Ashe's juniper and eastern red cedar reportedly occur in Texas, specifically in the Edwards Plateau (Hall 1952). Hybridization could be occurring within CBSP since many of the sampled individuals had trunk and abaxial gland characteristics that were mixed between Ashe's juniper and eastern red cedar. Junipers cause significant problems for native species (Diggs et al. 1999) by competing for plant-growth resources (Corbett and Lashley 2017; Yager and Smeins 1999; Vickery 1991) and may have allelopathic attributes which could affect surrounding vegetation (Young and Bush 2009; Stipe and Bragg 1989).

In CBSP, junipers were dense and dominant, creating thick shrubby masses close to the river. Eastern red cedar can shade out herbaceous vegetation (Hoff et al. 2018) and dense canopies of Ashe's juniper can reduce proliferation and species diversity of understory vegetation (Young and Bush 2009), to the point where the herbaceous zone can be nonexistent under larger juniper trees (Yager and Smeins 1999). Ashe's juniper and eastern red cedar also use water year-round and are drought-tolerant species (Caterina et al. 2014). Eastern red cedar has been shown to flexibly exploit deep soil water during drought and switch to

shallow water sources when available (Eggemeyer et al. 2009). Both species of juniper utilize water excessively which can cause soils to dry out and competitively exclude vegetative species which need wetter soils (Vickery 1991). Junipers' scale-like leaves create substantial leaf area which can intercept up to 95% of precipitation specifically in a completely closed canopy of eastern red cedar (Caterina et al. 2014). While most studies on adverse effects of junipers have focused on exploitative competition for resources, interference competition utilizing allelopathic compounds has been observed. One study's finding suggested that Ashe's juniper affected the germination of side-oats grama (*Bouteloua curtipendula*) through the release of allelopathic compounds (Young and Bush 2009), and phytotoxins from eastern red cedar potentially decreased the germination of finger coreopsis (*Coreopsis palmata* Nutt.) in another study on allelopathic properties (Stipe and Bragg 1989).

Ashe's juniper, eastern red cedar, and other shrubby invasives can be managed in multiple ways, but if left unmanaged, these trees will negatively impact the riparian ecosystem, and potentially change forest succession into an abnormal juniper dominated system (Bidwell et al. 2016). The aquatic portion of a riparian ecosystem is especially susceptible to pesticides because they can inadvertently and easily enter the water system where they decompose into more toxic compounds and harm other organisms (TPWD 2017), therefore herbicides are not an ideal treatment for selective brush management along rivers. Prescribed fire might be an option for managing juniper encroachment into riparian forests, as these methods can be applied in small amounts or in coordination to limit collateral effects on native species (Nelle 2015). Seedlings and small eastern red cedar trees are fire-intolerant and would normally be removed by low-intensity surface fires if fires had not been suppressed across much of the country (Hoff et al. 2018). However, larger junipers become difficult to kill even with prescribed fire, while also increasing the risk of wildfires (Hoff et al. 2018) that persist long enough to reduce or eliminate more tolerant species. The combination of individual mechanical removal, which could be limited to felling of larger junipers and prescribing fire to small shrubs and trees could be effective in areas that are encroached upon. Focused brush management with these two methods would minimize soil disturbance and potential damage to other woody species. While these junipers do not resprout after cutting or burning (Diggs et al. 1999), reapplication to new growth from the seed bank or follow-through of any form of management is crucial for control of invasive species.

Successional Stages of the Forest at CBSP

When this property became a state park, decades of anthropogenic activities and disturbances were halted, and a preservation management regime was started by the state. Junipers, which were reported in the Edwards Plateau as early as the 1950s (Hall 1952), were preserved within the park area by extension. Each seral stage in the process of succession affects the microenvironment through cover and shade, organic litter, and chemical output, so that the most adaptive species outcompete and encroach on already present species of that given microenvironment (Vankat 1943). In 2019, the area sampled at CBSP was relatively undisturbed, lacked evidence of recent larger disturbances such as fire or recent flooding, and as a result, junipers had invaded into climax riparian forest. In the Balcones Canyonlands Preserve, about 70 km southeast of CBSP, Ashe's juniper growth rates ranged from 0.6 in (1.5 cm) to 1 in (2.5 cm) per decade (O'Donnell 2020). Eastern red cedar with 6 cm to 8 cm DBH trunks are estimated to be around 20 to 30 years old (SRS Forest Service). Given these estimates, the average DBH of junipers in CBSP would indicate that their invasion into the riparian forest began within the past two to three decades.

Riparian zones in the Edwards Plateau can be characterized by the following upper-canopy communities: bald cypress (*Taxodium distichum*) and sycamore (*Platanus occidentalis*), pecan and sugarberry, and elm (*Ulmus* spp.; Wagner 2004). Bald cypress, pecan, and sugarberry were listed as dominants in a floodplain forest along the Guadalupe River in the Edwards Plateau and considered to be representative of climax conditions for this area (Ford and Van Auken 1982). Bald cypress was not sampled or observed along the TXCO River at CBSP, sycamores and sugarberry were not common, pecan was

dominant, and cedar elm was dense. The proposed climax community for a remnant bottomland hardwood forest in the Cross Timbers was a sugarberry-cedar elm-green ash community (Barry and Kroll 1999), which was similar to the cedar elm-green ash community reported in the bottomland forest at TBFS (Nelson et al. 2018), and to the sugarberry-cedar elm-pecan community of the mixed-hardwood bottomland forest on the Bosque (Rosiere et al. 2013). Cedar elm and sugarberry are components of and often become dominants in climax forest (Jones-Lewey 2016; Van Auken and Bush 1985). Old growth individuals of pecan, cottonwood (*Populus* spp.), willow (*Salix* spp.), and sycamore (*Platanus* spp.) are often dominant trees (Barbour et al. 1987) but are moderately to highly intolerant pioneer species that can persist into climax bottomland forest (Rosiere et al. 2013). TEAM reports the sample area adjacent to the river predominantly as floodplain hardwood forest: upper canopy can consist of cedar elm, sugarberry, American elm, pecan, plateau live oak, bur oak, western soapberry, Arizona walnut, and green ash; and the understory can include mesquite, gum bumelia, roughleaf dogwood, red mulberry, Texas persimmon, and possumhaw. This floodplain hardwood forest type potentially represents the original vegetation along this part of the TXCO River, as our data reflects the existence of remnants of this forest type within the riparian zone.

CONCLUSIONS

The quantification of this bottomland-floodplain forest provided the first description of woody and herbaceous communities along a portion of the TXCO River in CBSP. The sampled area indicated a degraded habitat dominated by invasive plants and overly abundant wildlife. The plant assemblages of the bottomland-floodplain forest at CBSP indicate that the ecological services of erosion prevention, river stability, and protection from runoff are likely no longer adequately provided. For this reason, CBSP cannot be recommended as a reference site for restoration at this time. Mechanical removal of large junipers paired with prescribed fire treatments to smaller trees and shrubs are restoration strategies that could facilitate or maintain species composition of the remnant climax forest that is currently threatened by juniper invasion. Additionally, reduction of excessive populations of white-tailed deer and exotic ungulates, especially feral hogs, in creek areas of the Edwards Plateau would ease utilization on herbaceous forage species. Should these management practices be implemented, and the remnant plant species restored to a more historical balance, CBSP may serve as a reference site for riparian forests in the Edwards Plateau-West Cross Timbers ecocline.

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Trunk wood essential oil profile comparison of *Abies concolor* (Pinaceae) and *Abies grandis* (Pinaceae) from northern Idaho (USA)

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ABSTRACT

Abies concolor and *Abies grandis* are essential oil-bearing plants in the Pinaceae family. Essential oil produced through steam distillation of the trunk wood was examined to establish the essential oil profile from cultivated populations of both species in northern Idaho (USA). The resulting essential oils ($n = 6$) were analyzed by GC/MS and GC/FID. Prominent volatile compounds (averages) from *A. concolor* trunk wood include α -pinene (12.2%), camphene (8.5%), β -pinene (29.0%), δ -3-carene (9.7%), limonene (5.1%), and bornyl acetate (9.4%). Prominent volatile compounds (averages) from *A. grandis* trunk wood include tricyclene (2.4%), α -pinene (11.8%), camphene (23.4%), β -pinene (11.0%), δ -3-carene (2.3%), limonene (8.5%), and bornyl acetate (17.5%). Comparing the two species, trunk wood essential oil profiles are similar, with 6 prominent volatile compounds in common. However, key volatile markers differentiate each species and could be used for future chemotaxonomic investigations. *Published online www.phytologia.org Phytologia 104(4): 66-73 (December 21, 2022). ISSN 030319430.*

KEY WORDS: *Abies concolor*, *Abies grandis*, aromatic profile, chemotaxonomy, conifer, essential oil, trunk, Pinaceae.

Abies concolor (Gordon & Glend.) Lindl. Ex Hildebr. and *Abies grandis* (Douglas ex D. Don) Lindl. are aromatic fir trees in the Pinaceae family (The World Flora Online 2022).

Abies concolor has a native range that spans western North America, the southern Rocky Mountains, and south to northern Mexico (Auders and Spicer 1990; Cronquist et al. 1972; Laacke 1990). However, throughout its widespread distribution, there exist many isolated pockets, both geographically and genetically, of native populations (Flora of North America 1993). *Abies concolor* trees grow at elevations between approximately 600 to 4000 meters and reach about 60-70 meters in height, with a smooth bark with elongated markings. The 2-2.5 mm wide curved needles are bluish green in color on both adaxial and abaxial surfaces (Auders and Spicer 1990; Cronquist et al. 1972).

Abies grandis is the tallest of the fir species and grows to a height of approximately 80 meters. This species is native to moist forests of the northwestern United States and southwest Canada and is found anywhere from sea level to 1800 meters elevation (Auders and Spicer 1990; Flora of North America 1993). Populations are described as morphologically and chemically uniform (Flora of North America 1993). The 2 mm wide and 20-35 mm long needles are a glossy dark green color on the adaxial surface and a greenish white on the abaxial surface, with a sharp tip at the end (Auders and Spicer 1990).

Conifers have been used by native peoples of British Columbia as medicine for respiratory illnesses and dermatological ailments in the form of tonics and external poultices, respectively, as well as for bedding and ground cover in living quarters (Turner 1998; Turner and Hebda 1990). In south-central Colorado, native peoples used *A. concolor* resin on skin blemishes or would mix resin with sugar to create a drink to fight urinary tract infections (Bye and Linares 1986). Salishan elders (Vancouver Island) drank *A. grandis* bark infusions to treat several ailments including tuberculosis, ulcers, colds, and stomach issues (Turner and Hebda 1990). The Southern Kwakiutl Indians of British Columbia collected pitch from young trees to create tonics for coughs, tuberculosis and as a laxative. Southern Kwakiutl Indians also held pieces of the root in their mouths to remedy canker sores (Turner and Bell 1973). In more recent history, the culinary world refers to *A. grandis* as the “grapefruit pine” because of its aromatic profile and citrus flavor (Valerón et al. 2021). The wood of both species is considered light and nondurable, and is used for woodworking and pulp, rather than construction (Uphof 1968).

The essential oil profile of both *Abies spp.*, extracted from foliar portions, cones, and/or cortical specimens, has been previously analyzed and established. *Abies concolor* leaf and cone essential oils have been found to be primarily composed of α -pinene, camphene, β -pinene, limonene, and bornyl acetate (Adams et al. 2011; Swor et al. 2022; Wajs-Bonikowska et al. 2017). *Abies grandis* leaf essential oil has been found to be primarily composed of α -pinene, camphene, β -pinene, β -phellandrene, and bornyl acetate (Adams et al. 2015; Zavarin et al. 1977). To the best knowledge of the authors, the essential oil profiles of the trunk wood has not been previously established in full for either species. Previous research on evergreen species in the Caprifoliaceae and Pinaceae families has shown that trunk wood essential oil often has a different essential oil profile than other portions of the tree, and often contains unique compounds that can be used for chemotaxonomic investigations (Poulson et al. 2020, 2021; Wilson et al. 2019, 2021). The current study establishes essential oil profiles for samples extracted from the trunk wood of both *A. concolor* and *A. grandis*, and provides an integrative tool for chemotaxonomic investigations.

MATERIALS AND METHODS

Abies grandis and *Abies concolor* plant material was collected from privately owned cultivated tree farmland in Bonner County, Idaho, USA. *Abies grandis* plant material was collected December 14, 2021 (48°34'40.1" N 116°26'56.7" W; 680 m elevation). *Abies concolor* plant material was collected February 8, 2022 (48°28'13.0" N 116°27'36.1" W; 674 m elevation). Four trees of each species were cut approximately halfway up the trunk utilizing the stump culture technique (Wunderlich 2020). Only the trunk material was used for this research, which includes the inner and outer bark, cambium, sapwood, and heartwood sections. Representative voucher samples used for identification are held in the University of Idaho Stillinger Herbarium in Moscow, ID, USA, and the Consortium of Pacific Northwest Herbaria in Seattle, WA, USA.

The plant material was prepared for distillation as follows (Figure 1). The limbs were removed flush against the trunks, leaving only the main tree trunk with no needles or limb material. The plant material, which included four trees (average age of nine years – determined by dendrochronology) for each species, was chipped with a woodchipper, blended, and stored in an airtight container at -20 ± 2 °C until steam distilled. Three separate steam distillations were performed on the prepared chips for each species, resulting in a total of six distillations for this study. The distillations were conducted in a 12 L food grade stainless steel distillation chamber with approximately 2.5 liters of water added to the chamber. Steam was passed through suspended chips for two hours after pass-over and the essential oil was separated from hydrosol using a cooling condenser and collected in an analytical graduated cylinder. The essential oil was stored in a sealed amber glass bottle until analysis.

Essential oil samples were analyzed, and volatile compounds identified, by GC/MS using an Agilent 7890B GC/5977B MSD (Agilent Technologies, Santa Clara, CA, USA) and Agilent J&W DB-5, 0.25 mm

\times 60 m, 0.25 μ m film thickness, fused silica capillary column. Operating conditions: 0.1 μ L of sample (20% soln. for essential oils in ethanol), 100:1 split ratio, initial oven temp. of 40 $^{\circ}$ C with an initial hold time of 5 min., oven ramp rate of 4.5 $^{\circ}$ C per min. to 310 $^{\circ}$ C with a hold time of 5 min. The electron ionization energy was 70 eV, scan range 35–650 amu, scan rate 2.4 scans per sec., source temp. 230 $^{\circ}$ C, and quadrupole temp. 150 $^{\circ}$ C. Volatile compounds were identified using the Adams volatile oil library (Adams 2007) using Chemstation library search in conjunction with retention indices. Note that limonene/ β -phellandrene/1,8-cineole, bornyl acetate/2-undecanone, β -cubebene/ β -elemene, and fenchone/terpinolene elute as single peaks. Their amounts were determined by the ratio of masses 68 and 79 (limonene), 77 and 93 (β -phellandrene), 81 and 108 (1,8-cineole), 69 and 81 (fenchone), 93 and 121 (terpinolene), 95 and 121 (bornyl acetate), 58 and 71 (2-undecanone), 105 and 161 (β -cubebene), and 81 and 93 (β -elemene). Volatile compounds were quantified and are reported as a relative area percent by GC/FID using an Agilent 7890B GC and Agilent J&W DB-5, 0.25 mm \times 60 m, 0.25 μ m film thickness, fused silica capillary column. Operating conditions: 0.1 μ L of sample (20% soln. for essential oils in ethanol, 1% for reference compounds in ethanol, 0.1% soln. for C7–C30 alkanes in hexane), 25:1 split ratio, initial oven temp. of 40 $^{\circ}$ C with an initial hold time of 2 min., oven ramp rate of 3.0 $^{\circ}$ C per min. to 250 $^{\circ}$ C with a hold time of 3 min. Essential oil samples were analyzed in triplicate by GC/FID to ensure repeatability (standard deviation < 1 for all compounds). Compounds were identified using retention indices coupled with retention time data of reference compounds (MilliporeSigma, Sigma-Aldrich, St. Louis, MS, USA).

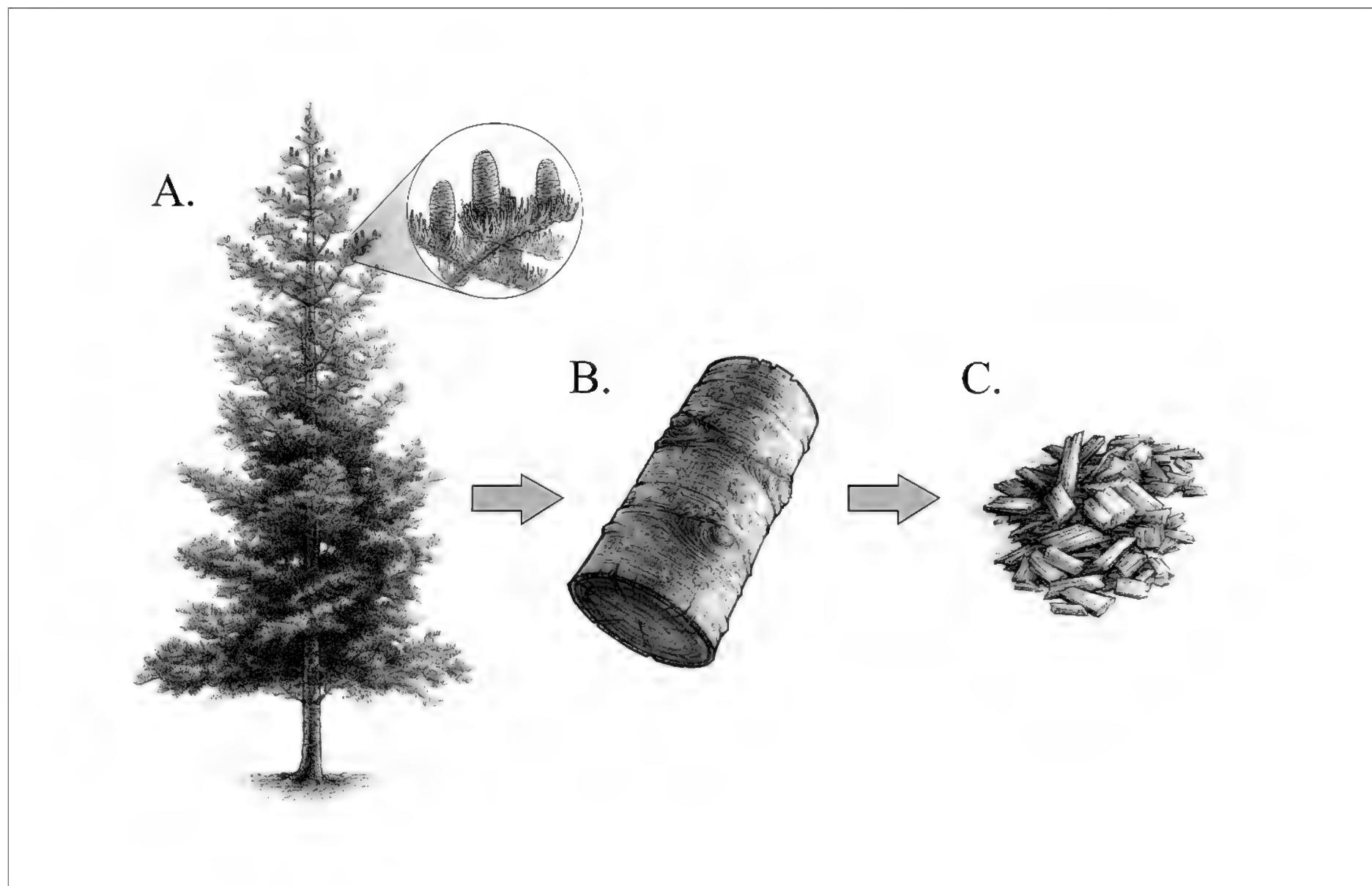


Figure 1. Botanical illustration of *Abies concolor* plant material collection and processing (plant material for both species was collected and processed identically). The tree (A) was felled according to the stump culture technique (Wunderlich 2020), all limbs removed flush against the trunk (B), trunk sections were chipped and blended (C), and stored at -20 ± 2 $^{\circ}$ C until steam distillation. Illustrated by Zach Nielsen, Utah Valley University (Orem, UT, USA).

RESULTS AND DISCUSSION

The aromatic profile of both *Abies concolor* and *Abies grandis* trunks were determined by GC/MS and GC/FID, and are detailed in Table 1. Prominent volatile compounds (averages) from *A. concolor* trunk wood include α -pinene (12.2%), camphene (8.5%), β -pinene (29.0%), δ -3-carene (9.7%), limonene (5.1%), and bornyl acetate (9.4%). Prominent volatile compounds (averages) from *A. grandis* trunk wood include tricyclene (2.4%), α -pinene (11.8%), camphene (23.4%), β -pinene (11.0%), δ -3-carene (2.3%), limonene (8.5%), and bornyl acetate (17.5%). The essential oil profile of both *Abies spp.*, extracted from foliar portions, cones, and/or cortical specimens, has been previously analyzed and established. However, to the best knowledge of the authors, the essential oil profiles of the trunk essential oils have not been previously established for either species. Previously studied *A. concolor* leaf and cone essential oils have been found to be similar to the trunk essential oil analyzed in this study, with all samples being primarily composed of α -pinene (leaf/cone 11.2-20.5%; trunk 12.2%), camphene (leaf/cone 7.5-25.9%; trunk 8.5%), β -pinene (leaf/cone 24.2-52.0%; trunk 29.0%), δ -3-carene (leaf/cone 5.5-6.5%; trunk 9.7%), limonene (leaf/cone 5.4-6.9%; trunk 5.1%), and bornyl acetate (leaf/cone 14.6-22.1%; trunk 9.4%) (Adams et al. 2011; Swor et al. 2022; Wajs-Bonikowska et al. 2017). Previously studied *A. grandis* leaf essential oil has also been found to be similar to the trunk essential oil analyzed in this study, with all samples being primarily composed of α -pinene (leaf 4.4-7.4%; trunk 11.8%), camphene (leaf 8.3-11.5%; trunk 23.4%), β -pinene (leaf 20.3-31.0%; trunk 11.0%), and bornyl acetate (leaf 12.7-26.2%; trunk 17.5%) (Adams et al. 2015; Zavarin et al. 1977). The differences are the prominence of limonene (leaf 0.8-2.5%; trunk 8.5%) and β -phellandrene (leaf 13.7-25.2%; trunk 1.1%) in foliar and trunk samples of *A. grandis* essential oil. The overall similarity in essential oil profiles, when comparing extracts from different plant parts of the same species, may be characteristic of plants in the Pinaceae family (Poulson et al. 2020).

Many of the minor compounds differentiate the trunk essential oil profiles of *A. concolor* and *A. grandis* from each other. While santene is only present in traces in *A. concolor* essential oil, it comprises 0.5% (avg.) of *A. grandis* essential oil. The opposite is found with linalool; which comprises 0.9% (avg.) of *A. concolor*, but is only detected in traces in *A. grandis* essential oil. Examining the entire essential oil profile, 28 compounds are detected in one species but not the other, and could be used for chemotaxonomy. Those found in *A. concolor* essential oil, but not in *A. grandis*, include fenchone, trans-pinocarveol, pinocamphone, myrtenol, thymol methyl ether, cumin aldehyde, cis-3-en-5-one, γ -muurolene, trans-nerolidol, β -calacorene, caryophyllene oxide, cedrol, cis-14-nor-muurol-5-en-4-one, and manool oxide. Those found in *A. grandis* essential oil, but not in *A. concolor*, include ethyl isovalerate, ethyl octanoate, 2-undecanone, citronellic acid, β -elemene, γ -elemene, 6,9-guaiadiene, cardina-3,5-diene, δ -selinene, α -selinene, trans-cadina-1,4-diene, germacrene B, intermedeol, and farnesol acetate. These key differences in trunk essential oil profile have been previously used to distinguish and identify plant species when traditional taxonomic methods cannot be used, such as when identifying trees burnt in wildfires (Wilson et al. 2021).

While many of the prominent compounds in the essential oils extracted from the trunk of these two species are the same, their relative abundance varies greatly. In *A. concolor* essential oil, α -pinene, β -pinene, and δ -3-carene were detected at higher relative percentages. In *A. grandis* essential oil, camphene, limonene and bornyl acetate were detected at higher relative percentages. The relative percent differences of the same compounds found in the two species varies greatly, being as low as 3.0 (α -pinene) and as high as 122.3 (δ -3-carene) (Table 2). These differences in compound abundance could also potentially be used for future chemotaxonomic investigations.

Table 1. Aromatic profile of *Abies grandis* and *Abies concolor* essential oil from trunk material only. Compounds not detected in a sample are denoted as not detected (ND) and those with values less than 0.1% are denoted as traces (tr). Compounds less than 1.0% that were unidentified are not included. KI is the Kovat's Index using a linear calculation on the DB-5 column (Adams 2007), those in bold font were calculated using an alkane standard. Relative area percent is determined by GC-FID. All essential oil samples were analyzed in triplicate to ensure repeatability (SD <1).

Compound Name	KI	<i>Abies concolor</i>			<i>Abies grandis</i>		
		1	2	3	1	2	3
ethyl isovalerate	849	ND	ND	ND	0.2	0.2	0.2
santene	884	tr	tr	tr	0.4	0.6	0.6
tricyclene	921	1.0	0.7	0.9	2.3	2.4	2.4
α -thujene	924	0.2	0.1	0.2	0.1	0.1	0.1
α -pinene	932	13.0	10.4	13.3	11.9	11.4	12.2
camphene	946	9.4	7.4	8.8	22.6	23.5	24.2
sabinene	969	0.3	0.2	0.3	0.2	0.2	0.2
β -pinene	974	32.2	25.3	29.5	11.1	10.6	11.3
myrcene	988	1.1	1.0	1.2	0.5	0.6	0.6
δ -3-carene	1008	11.3	8.6	9.2	2.0	2.4	2.6
α -cymene	1022	0.5	0.5	0.5	0.2	0.1	0.2
limonene	1024	6.4	3.9	4.9	7.1	9.6	8.8
β -phellandrene	1025	0.8	2.3	2.1	0.8	0.8	1.7
1,8-cineole	1026	tr	tr	tr	0.1	0.1	0.1
fenchone	1083	0.3	0.5	0.4	ND	ND	ND
terpinolene	1086	0.3	0.2	0.2	0.1	0.3	0.3
linalool	1095	0.7	1.2	0.9	tr	tr	tr
endo-fenchol	1114	0.2	0.2	0.2	tr	tr	tr
trans-pinocarveol	1135	0.2	0.6	0.2	ND	ND	ND
camphor	1141	0.3	0.4	0.3	0.7	0.6	0.6
camphene hydrate	1145	1.3	1.9	1.5	0.6	0.5	0.4
pinocarvone	1160	0.2	0.3	0.2	ND	ND	ND
borneol	1165	0.2	0.8	0.6	0.5	1.3	1.1
terpinen-4-ol	1174	0.2	0.5	0.4	0.1	0.1	0.1
ρ -cymen-8-ol	1179	0.2	0.2	0.1	0.1	tr	tr
cryptone	1183	0.5	1.0	0.6	0.4	0.1	0.2
α -terpineol	1186	0.3	0.5	0.4	0.1	0.1	0.1
myrtenol	1194	0.3	0.5	0.3	ND	ND	ND
ethyl octanoate	1196	ND	ND	ND	0.1	0.1	0.1
endo-fenchyl acetate	1218	0.1	0.2	0.2	tr	tr	tr
citronellol	1223	0.6	1.1	0.9	0.3	0.5	0.4
thymol methyl ether	1232	tr	0.1	0.1	ND	ND	ND
cumin aldehyde	1238	0.1	0.2	0.1	ND	ND	ND
piperitone	1249	0.1	0.1	0.1	tr	tr	tr
p-menth-8-en-3-ol acetate	1270	0.1	0.2	0.1	0.1	0.1	0.1

bornyl acetate	1284	7.8	11.5	8.9	19.8	17.0	15.7
2-undecanone	1293	ND	ND	ND	0.1	0.1	0.1
cis-3-en-5-one	1305	0.4	0.4	0.3	ND	ND	ND
citronellic acid	1312	ND	ND	ND	0.1	0.1	0.1
α -cubebene	1348	0.4	0.5	0.5	0.8	0.8	0.7
citronellyl acetate	1350	0.8	1.8	1.6	1.2	1.0	0.9
neryl acetate	1359	0.1	0.6	0.4	0.6	0.5	0.5
α -copaene	1374	0.3	0.4	0.4	0.6	0.5	0.5
β -cubebene	1387	0.2	0.1	0.2	0.5	0.4	0.4
β -elemene	1389	ND	ND	ND	0.1	0.1	0.1
(E)-caryophyllene	1417	0.1	0.1	0.2	0.4	0.4	0.3
γ -elemene	1434	ND	ND	ND	0.3	0.4	0.3
6,9-guaiadiene	1442	ND	ND	ND	0.1	0.1	0.1
cadina-3,5-diene	1449	ND	ND	ND	0.1	0.1	0.1
α -humulene	1452	0.0	0.2	0.0	0.1	0.1	0.1
cis-cadina-1(6)-4-diene	1461	ND	ND	ND	0.1	0.1	0.1
γ -muurolene	1478	0.1	0.5	0.1	ND	ND	ND
β -selinene	1489	tr	tr	tr	0.3	0.3	0.3
δ -selinene	1492	ND	ND	ND	tr	0.1	0.1
epi-cubebol	1492	0.6	0.4	0.5	1.2	1.1	1.1
α -selinene	1498	ND	ND	ND	0.1	0.1	0.1
α -muurolene	1500	0.3	0.4	0.4	0.5	0.4	0.4
cubebol	1514	1.1	0.6	0.7	1.8	1.7	1.9
δ -cadinene	1522	0.5	0.6	0.6	1.7	1.7	1.4
trans-cadina-1,4-diene	1533	ND	ND	ND	0.1	0.1	0.1
germacrene B	1559	ND	ND	ND	0.2	0.2	0.2
trans-nerolidol	1561	1.1	1.8	1.5	ND	ND	ND
β -calacorene	1564	0.1	0.5	0.1	ND	ND	ND
caryophyllene oxide	1582	0.1	0.2	0.1	ND	ND	ND
gleenol	1586	0.1	0.1	0.1	0.1	0.1	0.1
cedrol	1600	tr	0.1	0.1	ND	ND	ND
1,10-di-epi-cubenol	1618	0.4	0.6	0.5	0.9	0.9	0.9
1-epi-cubenol	1627	0.1	0.3	0.2	0.3	0.3	0.3
intermedeol	1665	ND	ND	ND	0.5	0.5	0.5
cis-14-nor-muurol-5-en-4-one	1688	0.1	0.1	0.1	ND	ND	ND
farnesol acetate	1830	ND	ND	ND	0.4	0.4	0.3
manool oxide	1987	0.1	tr	0.2	ND	ND	ND
Totals		97.2	93.2	96.1	95.9	95.8	96.3

Table 2. The relative area % of prominent compounds in *Abies concolor* and *Abies grandis* essential oil, averaged across all samples. The relative percent difference (RPD) is provided.

Shared Prominent Compounds	<i>Abies concolor</i> (avg.)	<i>Abies grandis</i> (avg.)	RPD
α-pinene	12.2	11.8	3.0
camphene	8.5	23.4	93.3
β-pinene	29.0	11.0	89.8
δ-3-carene	9.7	2.3	122.3
limonene	5.1	8.5	50.1
bornyl acetate	9.4	17.5	60.2

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